ORGANIC MATTER SOURCES ON THE CHUKCHI SEA SHELF IN A CHANGING ARCTIC

By

Ann-Christine Zinkann, M.S.

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APPROVED:

Katrin Iken, Committee Chair
Matthew Wooller, Committee Member
Seth Danielson, Committee Member
Mary Beth Leigh, Committee Member
Georgina Gibson, Committee Member
Lara Horstmann, Department Chair
Department of Marine Biology
Bradley Moran, Dean
College of Fisheries and Ocean Sciences
Michael Castellini, *Dean of the Graduate School*

Abstract

Climate-change induced alterations of the organic matter flow from various primary production sources to the benthic system in the Arctic Chukchi Sea could have major implications on carbon cycling, sequestration, and benthic food web structure sustaining upper trophic levels. In particular, the role and contribution of terrestrial matter and bacterial matter could become more prominent, with increasing erosion and permafrost melt being discharged from land, and warming water temperatures raising bacterial metabolism. In this study, I used essential amino acid (EAA) specific stable isotope analysis to trace the proportional contributions of bacterial, phytoplankton, and terrestrial organic matter in sediments, as well as benthic invertebrates on the Chukchi Sea shelf. Across the upper 5 cm of sediments, most organic matter sources were equally distributed, except for a slight decrease with depth in phytoplankton EAA. Terrestrial sources contributed the majority of EAA (~76 %) in all sediment layers, suggesting a potential accumulation of this material due to slow degradation processes. These results indicate a well-mixed upper sediment horizon, possibly due to bioturbation activity by the abundant benthos. Experimental observations of increases in bacterial production, measured as phospholipid fatty acid (PLFA) production, at water temperatures 5 °C above ambient (0 °C) and under sufficient substrate conditions suggest that bacterial organic matter in sediments could become a greater organic matter source in the sediments of a future, warmer Arctic. EAA source contribution to various benthic invertebrate feeding types (FT) were similar but showed significant differences among genera within the same FT, suggesting that feeding habits are more genus-specific rather than FT-specific. These differences were attributed to variations in other characteristics such as mobility, selectivity, and assimilation efficiency. Terrestrial EAA contributed high amounts to all benthic genera, supporting other recent findings that this source is readily utilized by benthic invertebrate consumers. These results of organic matter source contributions across sediments and benthic invertebrate feeding types were then used to better resolve the detrital pathways in an Ecopath mass-balance model of the Chukchi Sea. The incorporation of terrestrial matter as an organic matter source to Chukchi Sea food webs and updated organic matter use in benthic invertebrate diets balanced energy flow from phytoplankton and bacterial production through the food web. Simulations of potential future reductions of the pelagic production to the benthos negatively impacted benthic feeding taxa, which could be partially compensated by a simulated increase in terrestrial and bacterial organic matter supply.

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Dedication

This dissertation is dedicated to my parents, Irene and Harald, who have been a source of strength, support, inspiration, who continuously provided their support throughout this time. Thank you for everything and helping me live the life I love today.

General Introduction

The Arctic Ocean has been experiencing longer ice-free seasons and is predicted to be ice-free in the summer as early as 2040 (Overland and Wang, 2013; Laliberté et al., 2016). An increase in the ice-free period allows for increased heat fluxes that result in a further delay of ice formation in the fall, reducing the length of sea ice cover even more (Steele et al., 2008). Arctic shelf systems are experiencing warming three times the global average and are, therefore, especially vulnerable to these warming trends. Among all Arctic shelves, the Chukchi Sea shows one of the fastest declines in sea ice cover (Steele et al., 2008; Serreze et al., 2009; Frey et al., 2015). The Chukchi Sea is a highly productive region of the Arctic Ocean with traditionally long periods of seasonal sea ice cover, resulting in short seasonal pulses of ice-associated and pelagic primary production (Walsh et al., 1989; Gosselin et al., 1997). Almost 70 % of primary production remains ungrazed in the water column and sinks in tight pelagic-benthic coupling to the seafloor, supporting rich benthic communities (Walsh et al., 1989; Lovvorn et al., 2003; Piepenburg, 2005; Grebmeier, 2012). Climate-driven changes in the timing of sea ice retreat and rising temperatures could result in a shift in the timing and amount of ice-associated and pelagic production with a tendency towards smaller-celled phytoplankton communities. These shifts could enhance retention in the water column and increase grazing pressure by zooplankton, thus weakening pelagic-benthic coupling (Hunt et al., 2002; Lalande et al., 2007; Li et al., 2009; Arrigo and van Dijken, 2015).

Pelagic production is considered the main food source in Arctic benthic food webs, but additional sources, such as terrestrial matter and bacteria, active in organic matter processing, have recently been acknowledged as important contributors to the benthic food web (Dunton et al., 2006; Iken et al., 2010; McTigue et al., 2015; Bell et al., 2016). The influx of terrigenous material in the Arctic is controlled by coastal erosion, glacial melt, and river discharge (Guo et al., 2004; Goñi et al., 2005; Yunker et al., 2005). The Arctic Ocean receives disproportionately large river discharge (about 10 % of global discharge, Aagaard and Carmack, 1989), which has increased on average by ~2.6 % per decade since the 1970s (McClelland et al., 2006). In the Chukchi Sea, terrestrial organic matter can contribute over half of total sediment carbon across the shelf (Morris et al., 2015; Chapter 1). Additionally, bacteria play essential roles in organic matter processing (Arndt et al., 2013) and are also a vital source in benthic sediments, where they contribute nutritional value when associated with both sediment particles and microalgae (Garneau et al., 2009). As such, bacteria are indirectly ingested by benthic invertebrates when feeding on sediment or microalgae (e.g., Newell, 1965; Heip et al., 1995). While Arctic bacterial communities are adapted to low *in situ* temperatures, predicted warming of bottom water temperatures (Wang et al., 2012) could

increase optimal bacterial growth rates and production (Knoblauch et al., 1999; Kirchman et al., 2009; Wiklund et al., 2009; Kritzberg et al., 2010). Higher proportions of terrestrial matter and an increase in bacterial organic matter availability could enhance their role as a food source to benthic food webs, especially if phytoplankton export might be reduced (Kirchman et al., 2009; McMeans et al., 2013; Bell et al., 2016).

Organic matter provenance in marine sediments plays an essential role in long-term carbon sequestration and in providing a food source to benthic food webs (Muller-Karger, 2005; Chen and Borges, 2009; Smith et al., 2015). The main organic matter sources to marine shelf regions come from marine photosynthetic and terrestrial production (Hedges et al., 1997; Yunker et al., 2005). Once organic matter settles to the seafloor, sediment characteristics including grain size, permeability, and porosity influence the exchange of O_2 and nutrients with the overlying water column and can result in steep concentration gradients of biochemical properties (Klump and Martens, 1989; Santschi et al., 1990; Glud, 2008). These properties highly influence diagenetic processes of bacterial communities within the sediment, influencing patterns of long-term carbon storage (Rysgaard et al., 1998; Burdige, 2007; Arndt et al., 2013). Furthermore, the lability of organic matter that is supplied to the sediment influences degradation processes as structurally more complex components, e.g., terrigenous material, is more refractory than less complex components, such as from phytoplankton or bacterial sources (Hedges et al., 1997; Opsahl and Benner, 1997; Arndt et al., 2013). Additionally, bioturbation and bioirrigation processes of benthic consumers influence the distribution of excess organic matter within the sediment and enhance O_2 and nutrient exchange with the overlying water (Kristensen and Blackburn, 1987; Sun et al., 1993; Burdige, 2007; Bianchi et al., 2018). The processes of organic matter supply, degradation, and bioturbation can highly influence long-term carbon sequestration and availability of organic matter sources within the sediment for benthic consumers.

Benthic communities are an important energy link between settling organic matter and higher trophic levels and play a critical role in detrital degradation within the sediment (Hyland et al., 2005; Wrede et al., 2017). In areas such as the Chukchi Sea, the pulsed export of highly seasonal production results in a limitation of organic matter resources for the benthos, increasing competition within the benthic community (Levinton, 1972). This competition is partially reduced by differences in strategies of acquiring food sources on the seafloor, which are broadly categorized as feeding types (FT) (e.g., Hunt, 1925; Word, 1979; Jumars and Gallagher, 1982). The main FTs are suspension feeders (SF), surface deposit feeders (SDF), subsurface deposit feeders (SSDF), and predators/scavengers (P/S). Suspension feeders

capture fresh settling material or resuspended particles out of the water column (Sokolova, 1972; Walker and Bambach, 1974). Deposit feeders are separated into two categories, SDF that forage on deposited material on the sediment surface, and SSDF that exploit material in deeper sediment horizons (Lopez and Levinton, 1987). While P/S rely less directly on organic matter sources and instead actively hunt their prey or feed on dead organisms (e.g., Walker and Bambach, 1974; Bluhm et al., 2009), they are linked to the organic matter through their particle-feeding prey. These various feeding strategies suggest a potential for resource partitioning through reliance on different organic matter sources to different degrees among FT. If so, changes in the composition of organic matter supply to the seafloor due to climate change could have implications on the various FT, and the role they play in ecosystem function processes (Bremner et al., 2003; Węsławski et al., 2011; Kędra et al., 2015).

Ecosystem models are an effective tool to investigate ecosystem-scale processes, how different stressors might affect a system, and in the management of marine resources (Aydin and Mueter, 2007; Gaichas et al., 2011; Doney et al., 2012). Several ecosystem models have been developed for the Chukchi Sea, showing that major carbon flow occurs through the biomass-dominating benthic food web (Whitehouse, 2013; Whitehouse et al., 2014; Whitehouse and Aydin, 2016). However, the role of detrital organic matter, especially deriving from terrestrial sources, on the energy flow through the food web has not been resolved in current Chukchi Sea ecosystem models. Climate-induced changes in the relative proportions of pelagic production, terrestrial matter, and bacterial production on Arctic shelf system could result in shifts in benthic food web structure and impact the energy flow to higher trophic levels (e.g., Lohrer et al., 2012; Dayton et al., 2019).

This dissertation explored the role of three organic matter sources (bacterial, phytoplankton, terrestrial) in sediments, benthic invertebrates, and ecosystems modeling. Specifically, chapter 1 identified the proportional contributions of these organic matter sources in depth-stratified sediments (0 - 5 cm) and evaluated how sediment bacterial production might change at higher temperatures (5°C over currently ambient 0°C). Chapter 2 evaluated if the classification into feeding type is a useful concept to understand the use of various organic matter sources in benthic invertebrates across the Arctic Chukchi Sea. Lastly, chapter 3 used the results gathered in the previous chapters to improve a lower trophic benthic ecosystem model for the Arctic Chukchi Sea by including terrestrial organic matter as a source to the benthic food web and to evaluate how biomass of major ecosystem components (pelagic and benthic invertebrates, fishes, birds, marine mammals) respond to scenarios of future Arctic ecosystem conditions.

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Chapter 1: Digging deep: depth distribution of organic matter sources in Arctic Chukchi Sea sediments[1]

1.1 Abstract

Climate-induced changes in the composition of organic matter sources in Chukchi Sea sediments can have major implications on carbon cycling, carbon sequestration, and food sources for lower benthic trophic levels. The aim of this study was to identify the proportional contributions of organic carbon from primary producers (phytoplankton, terrestrial, and bacterial) to depth-stratified sediments (0 - 5 cm) across the Arctic Chukchi Sea shelf using essential amino acid (EAA) specific stable carbon isotope analysis. Across sediment depth strata, the majority of EAA in sediments (~76 %) originated from terrestrial sources and may be indicative of accumulation over time due to slow degradation processes of this source within sediments. The different EAA sources showed no significant differences in proportional contributions with sediment depth except for phytoplankton-derived EAA, which decreased with increasing sediment depth. These patterns indicate a well-mixed upper sediment horizon, possibly from bioturbation activities by the abundant benthos. EAA source distributions had no relationship with environmental variables across the Chukchi shelf. The response of bacterial production to elevated temperatures was tested experimentally, using phospholipid fatty acid (PLFA) analysis. Bacterial production was initially higher at 5°C over 0°C; however, a drawdown of substrate or potential increase in predation activity and viral lysis resulted in bacterial production to be the same at both temperature settings. Determining the base line of organic matter source presence in marine sediments is key in the identification of potential future shifts in organic matter supply to sediments with climate induced changes. Identifying base lines and potential shifts in e.g., bacterial production with changes in temperature can aid in the understanding of the consequences of climate change in terms organic matter presence and flow through benthic consumers that utilize these shelf sediments as feeding grounds.

Keywords: Stable isotope fingerprinting, phospholipid fatty acids, terrestrial organic matter, bacterial production

1.2 Introduction

Marine sediments make up the majority of the ocean floor and, especially on continental shelves and margins, constitute the most important region of carbon cycling and long-term carbon sequestration

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in the world (Muller-Karger, 2005; Chen and Borges, 2009; Smith et al., 2015). Sediments play vital roles in small and large-scale processes, from understanding regional distribution of carbon sources, and their roles in benthic food webs, to global carbon budgets. Carbon provenance is essential to all these processes, with the main sources to marine shelf regions coming from marine photosynthetic and terrestrial production (e.g., Hedges et al., 1997; Yunker et al., 2005). Bacterial production from organic matter degradation is prominent within the sediments (Rysgaard et al., 1998). Sediment conditions highly influence the effects of bacterial degradation processes within the sediment and, thus, patterns of long-term refractory carbon storage or the release of bioavailable carbon (Burdige, 2007). Once organic matter has settled to the sediments, sediment properties such as grain size, permeability, and porosity drive the interactions at the sediment-water interface and diagenetic processes (Klump and Martens, 1989; Santschi et al., 1990; Arndt et al., 2013). For example, water velocities influence both sediment grain size and organic carbon composition in marine sediments. These sediment properties influence exchange of O_2 and nutrients with the overlying water column and can result in steep concentration gradients of biochemical properties with increasing sediment depth (Santschi et al., 1990; Glud, 2008).

Material derived from marine production is considered to contain large quantities of labile components, i.e., highly reactive and subject to fast degradation in sedimentary processes (Sun et al., 2007). Degradability decreases with increasing amounts of more structurally complex components, such as those found in terrigenous sources (Hedges et al., 1997; Opsahl and Benner, 1997; Arndt et al., 2013). Additionally, degradation processes within the sediment are enhanced in the presence of O_2 and rapidly decrease with decreasing O_2 concentrations. While part of the deposited organic carbon on marine shelf systems is readily utilized at the sediment surface, excess material can be drawn down into deeper sediment layers by bioturbation by the benthic community (Kristensen et al., 2012). Once it reaches deeper sediment layers, organic carbon provides both a food source for deeper sediment-dwelling organisms and is subject to microbial degradation processes. The interplay of deposition, bioturbation, and degradation processes within the sediment influence the quantity and distribution of different carbon sources among sediment layers. Understanding the carbon source distribution with sediment depth is important for considerations of long-term sequestration as well as availability of food sources for benthic organisms feeding within different sediment horizons.

Despite the Arctic being the smallest of the world's oceans, it receives a disproportionately large fraction of the global river discharge (about 10 %, Aagaard and Carmack, 1989), and its immense shelf areas play a major role in carbon sequestration (Stein and Macdonald, 2004). High biological productivity

is concentrated within a short seasonal cycle, while Arctic shelf regions receive large amounts of terrestrial carbon from river discharge, permafrost erosion, and glacial melt (e.g., Guo et al., 2004; Goñi et al., 2005; Yunker et al., 2005). Terrestrial input can make up close to half of the total carbon budget in some shelf seas of the Pacific Arctic, such as the Chukchi Sea (Belicka and Harvey, 2009), although this input is typically smaller than that from marine primary production (Stein and Macdonald, 2004). As accelerated climate change affects Arctic shelves, proportional carbon contributions from marine versus terrestrial production could shift in the future. For example, under historically cold conditions in the Chukchi Sea, a large proportion of the high primary production tended to be ungrazed in the water column and sank to the seafloor in tight pelagic-benthic coupling (Grebmeier and Barry, 1991). Effects of earlier sea ice retreat and rising temperatures could include a shift in phytoplankton composition towards smaller-celled communities, reducing export to the seafloor (Hunt et al., 2002; Li et al., 2009). Although overall phytoplankton production in the Arctic has increased in recent years due to a longer growing season (Arrigo et al., 2008; Wassmann and Reigstad, 2011; Hill et al., 2018), reduced water column production reaching the seafloor could strongly affect the proportion of this carbon source in sediments (Lalande et al., 2007). In contrast, an increase in river discharge, permafrost melt, and coastal erosion could carry increasing amounts of terrestrial carbon onto the shelf (Lantuit et al., 2012). Increases in terrestrial matter on Arctic shelves could cause an increase in food web steps from additional bacterial degradation, decreasing the amount of carbon availability to higher trophic levels and reducing trophic efficiency of the whole food web (Dunton et al., 2006). Alternatively, terrestrial matter could become an additional carbon source for benthic food webs after microbial degradation, thus increasing overall benthic food supply (Bell et al., 2016).

Among the plethora of possible bacterial metabolic pathways, conversion of particulate and dissolved organic carbon (POC and DOC, respectively) into bacterial cells (bacterial production) is especially important to build bacterial biomass in marine sediments that can be utilized by benthic organisms as food (Jiao et al., 2010). Generally, bacterial biomass decreases with sediment depth as labile carbon availability decreases and more refractory portions increase (Fabiano and Danovaro, 1994). In addition to the carbon quality, O_2, and nutrients to support redox-reactions, bacterial production is also reliant on temperature (Mermillod-Blondin et al., 2004; Kristensen et al., 2012; North et al., 2014). While Arctic bacterial communities are adapted to low *in situ* temperatures, their optimal production rate is typically above polar temperatures (Knoblauch et al., 1999). Bacterial degradation of POC requires production of extracellular enzymes; however, at low temperatures hydrolyzing efficiency decreases, resulting in less substrate made available (Arnosti and Jorgensen, 2003). Bottom water temperatures on

Arctic shelves are predicted to increase to 5°C by 2050 (Wang et al., 2012), which may increase bacterial production and biomass in sediments substantially (Kirchman et al., 2009; Wiklund et al., 2009; Kritzberg et al., 2010). A higher proportion of bacterial carbon in marine sediments could increase their role as a food source for benthic organisms and change the proportions of the various carbon sources in Arctic shelf sediments.

The aim of this study was to identify the proportional contributions of carbon sources (phytoplankton, terrestrial, and bacterial carbon) within the top 5 cm horizon of sediments across the Chukchi Sea shelf. We hypothesized that the relative proportions of carbon sources across the shelf would vary spatially in response to environmental conditions. We further predicted that the proportions of phytoplankton-derived carbon would be highest in surface sediments while proportions of bacterial and terrestrially derived carbon would be higher in deeper sediment layers. Additionally, we hypothesized that higher temperatures (5°C over ambient 0°C) would result in higher bacterial community production within sediments.

1.3 Materials and Methods

1.3.1 Sample collection

Sediment samples used to examine carbon sources were collected at 14 stations between 30 and 54 m water depths across the Chukchi Sea shelf during the Arctic Marine Biodiversity Observing Network (AMBON, www.ambon-us.org) cruise in August 2015 (Fig. 1.1). Single sediment samples were collected with a Haps core at stations where the core could penetrate the sediment. The top 5 cm of each core was sliced into 1 cm sections, each layer was then homogenized with a spatula, and frozen at -20°C in whirl packs. Sediment samples were transported frozen to the University of Alaska Fairbanks for later processing.

Contextual environmental variables, measured concurrently by collaborators at each station, included bottom temperature, bottom salinity, sediment grain size, sediment chlorophyll *a* content, total organic carbon (TOC), bulk sediment C/N ratios, and bulk stable carbon and nitrogen isotope compositions (expressed as $\delta^{13}C$ and $\delta^{15}N$ values). Environmental data are available through the Marine Biodiversity Observing Network (MBON) Data Portal (https://mbon.ioos.us/, https://doi.org/10.25921/zqwr-at45). Bottom temperature and salinity ranged from -1.7°C to 7.5°C and 31.0 to 32.7, respectively. The majority of the sediments consisted of silt (phi ≥5, 17.5 – 97.1 %, median 74.3 %) with varying proportions of sand (phi 1-4, 2.7 – 82.3 %, median 24.6 %). Chlorophyll *a* concentration of the upper 2 cm sediment layer

ranged from 5.5 to 17.4 mg/m^2 and TOC ranged from 0.25 to 1.35 %. Surface sediment bulk C/N (wt/wt) ratios ranged from 4.01 to 8.74 and $\delta^{13}C$ and $\delta^{15}N$ values ranged from -21.2 to -24.4 ‰ and 4.8 to 9.8 ‰, respectively.

Sediment samples for microcosm experiments of bacterial production were collected at one location in the northern Bering Sea (63.316643 °N, -168.467905 °W) during the Arctic Shelf Growth, Advection, Respiration, and Deposition Rate Measurements (ASGARD) cruise in 2017. The upper 1 cm of eight Haps cores were taken and homogenized. Bottom water from the sediment sampling site was collected using a CTD rosette and filtered through GF/F filters (Whatman, approx. pore size 0.7 µm) to remove particles. Homogenized sediments in whirl packs were topped off with filtered seawater and stored at 0°C onboard the vessel for three days before returning back to the University of Alaska Fairbanks (UAF) for experimental set up.

1.3.2 Determining organic matter sources using essential amino acid stable isotope analysis

Essential amino acid (EAA) specific stable isotope fingerprinting was used to identify carbon sources in sediments. This approach is based on the EAA of phylogenetically close groups (e.g., marine microalgae, terrestrial plants, bacteria) conserving specific stable isotope values that form characteristic patterns for these groups (Larsen et al., 2013; Larsen et al., 2015). For EAA extraction, homogenized sediment layers were freeze-dried for 24 h and dry weight per sample determined (150-220 mg). Dried sediments were transferred into culture tubes, 1 mL of 6-N hydrochloric acid (HCl) added, flushed with N_2 to prevent oxidation, sealed and hydrolyzed at 110°C in a heating block for 20 h (following Larsen et al., 2013). The liquid phase containing amino acids (AA) was transferred into a 3 mL BD syringe™ connected to a 0.2 µm Millex-GP™ filter to remove any excess sediment material. The syringe filter was rinsed with approximately 0.25 µl of 0.1-N HCl to remove remaining AA. Norleucine (Sigma-Aldrich, batch number BCBQ0497V) (25 µl) was added as an internal standard to each sample to enable later quantification of AA, and samples were evaporated to dryness under constant N_2 flow in a 60°C water bath. A cation exchange column equipped with Dowex 50WX8-400 ion exchange resin was prepared for each sample, rinsed with 0.01 N HCl, and each sample resuspended in 1 mL 0.01-N HCl, and added to its respective column. Amino acids in the sample solution remained on the resin. Bound AA were rinsed from the column with 4 mL 2-N ammonium hydroxide (Na_4OH) in 1 mL increments and the combined eluents collected. These samples were then dried under constant N_2 flow in an 80°C water bath for 2-4 h. Amino acid in samples were re-protonated by adding 1 mL 0.2-N HCl, the sample then flushed with N_2, heated for 5 min at 110°C, and evaporated to dryness. Dried samples were acetylated using 2 mL acidified 2-propanol to

convert non-volatile AA into volatile N-acetyl methyl ester derivatives, and samples capped and heated to 110°C on a heating block for 60 min. After cooling, samples were evaporated to dryness under constant N_2 flow at 60°C. Samples were washed twice with 0.5 mL dichloromethane (DCM) and evaporated to dryness at room temperature under a constant stream of N_2. Samples were derivatized by adding 0.5 mL trifluoroacetic acid (N-TFA) and 0.5 mL DCM, heated at 100°C for 10 min, cooled, and evaporated to dryness at room temperature under a constant stream of N_2. Then, 2 mL phosphate-buffer (PB) and 2 mL chloroform were added to each sample, shaken for 60 sec, and centrifuged for 5 min at 600 g (3000 rpm). The chloroform layer (bottom layer) containing AA was transferred into new vials, while the remaining PB (top layer) was re-extracted twice with 1 mL chloroform each (repeat shaking and centrifuging). Derivatized AA were then dried at room temperature under N_2. To ensure full derivatization, 0.5 mL N-TFA and 0.5 mL DCM were added to each sample vial, heated at 100°C for 15 min, and then rinsed with DCM as described above. Ethyl acetate (250 µl) was added to each sample and transferred into 2 mL vials. $\delta^{13}C_{AA}$ values of AA were determined on a gas chromatograph isotope ratio mass spectrometer (GC-IRMS) equipped with an HP ULTRA-1 column (Agilent, 50 m x 0.32 mm x 0.52 µm) at the UAF Alaska Stable Isotope Facility (ASIF).

All AA samples were analyzed in triplicate and the following five essential and six non-essential (non-EAA) separated: isoleucine (Ile), leucine (Leu), phenylalanine (Phe), threonine (Thr), valine (Val) as EAA, and alanine (Ala), aspartic acid (Asp), glutamic acid (Glu), glycine (Gly), proline (Pro), and serine (Ser) as non-EAA. The additional EAA lysine (Lys) and tyrosine (Tyr) were not consistently detected in all samples due to low concentrations, and additional non-EAA histidine (His) and methionine (Met) were below detection levels in all samples. Only EAA were used in analyses to determine proportional contributions from various primary producer endmembers in sediments (e.g., Larsen et al., 2015) Additionally, a homogenized sample of the Arctic caridean shrimp *Sabinea septemcarinata* was extracted and analyzed for $\delta^{13}C_{AA}$ values of EAA along with each batch to account for analytical variability among different extraction batches.

1.3.3 Sediment bacterial production incubations

Phospholipid fatty acids (PLFA) were used to determine bacterial production at different temperatures in sediment microcosm experiments. PLFAs are a major component of bacterial cell membranes and a common biomarker used to identify the bacterial community and their biomass (Boschker et al., 1998; He et al., 2015). A ^{13}C-labeled and non-labeled microalgal stock was grown prior to the ASGARD cruise at UAF according to Weems et al., (2012), to be used as substrate in microcosm

experiments. An 8-L monoculture of the marine diatom *Chaetoceros muelleri*, supplied by Dr. R. Hopcroft (UAF), was incubated at 5°C with 24 h light over a one-month period. Artificial seawater (Instant Ocean, S=32) served as a medium to grow algal culture, and nutrient fertilizer (Guillard's f/2 marine water enrichment + silicate, concentration 50x) was added weekly (160 mL). Aeration and mixing were provided by bubbling the culture with an aquarium pump. The culture was subsampled weekly, at which time half of the batch was removed and replaced with artificial seawater and f/2 nutrients. The removed algal stock (4 L) was subsampled, with 2 L being centrifuged (4000 rpm, 2647 g, 5 min) and resulting pellets frozen at -20°C for the non-labeled algal stock. The remaining 2 L were incubated for another 24 h with 1 mL of ^{13}C-enriched sodium bicarbonate solution (1.7 g of 98 % ^{13}C sodium bicarbonate in 100 mL distilled water added to 2 L culture) and afterwards centrifuged (4000 rpm, 2647 g, 5 min), and frozen at -20°C for isotopically labeled algal stock. Multiple harvested batches of algae were homogenized to ensure a consistent algal food stock supplied to the microcosm treatments. Bulk carbon stable isotope values of algal stocks were determined using a GC-IRMS to ensure sufficient isotopic enrichment and for later calculation of carbon incorporation into bacterial PLFAs. The average bulk stable isotope value ($\delta^{13}C$) for the labeled algal stock was 2300.0 ‰, while the non-labeled algal stock averaged at -14.9 ‰.

About 35 g (wet weight) homogenized sediment were placed into 50 mL Erlenmeyer flasks, and each flask was covered by approximately 30 mL of ambient filtered seawater. Erlenmeyer flasks were loosely covered with aluminum foil to prevent contamination and then randomly assigned to one of two temperature treatments. Temperature settings were chosen to be 0°C (Treatment 1), representing current bottom water temperature on the Chukchi Sea shelf for much of the annual cycle (Weingartner et al., 2013), and 5°C, as a predicted increased bottom water temperature on the shelf by 2050 (Treatment 2) (Wang et al., 2012). Flasks were then placed on a shaker in the incubator at the respective temperatures to ensure sufficient O_2 supply during the experiment. Isotopically labeled algal stock was supplied to half the 0°C and half the 5°C treatment flasks, while the other respective half received non-labeled algal stock. Algal stock was added at time zero (T_0) at the beginning of the experiment at a concentration of 458 mg C m^{-2}, reflecting typical *in situ* daily organic carbon deposition rates in the Chukchi Sea at the time of sampling (Moran et al., 1997). Both temperature treatments were run concurrently with labeled and non-labeled algal food in parallel; experiments were destructively sampled at eight times (0, 3, 6, 12, 24, 48, 96, and 192 h), when one flask per temperature and isotope label treatment was removed and contents frozen (-20°C) for later PLFA analysis.

Sediment PLFA extraction followed methods described by He et al., (2015). Sediment samples from the experiments were freeze-dried for 24 h and approximately 5.0 g sample sequentially extracted with 3.2 mL citric acid buffer, 4.0 mL chloroform, and 8.0 mL methanol. Then, 4.8 mL citric acid and 6.0 mL chloroform were added to the combined supernatants per sample, well shaken, and the sample kept at 4°C in the dark overnight for phase separation. The bottom chloroform layer containing lipids was isolated, washed with methanol, and dried under constant N_2 flow in a water bath (25-35°C). Through solid phase extraction (SPE) gel chromatography, both neutral lipids and glycolipids were removed using chloroform and acetone, respectively. Remaining polar PLFAs were collected using methanol and dried under constant N_2 flow in a water bath (25-35°C). PLFAs were esterified into fatty acid methyl esters (FAMEs) using methanol:toluene, potassium-hydroxide:methanol, n-hexane:chloroform, acetic acid, and deionized water, and 80 µL of internal 19:0 fatty acid standard (nonadecanoate, Sigma Aldrich, batch number BCBT3339) was added for later PLFA quantification. The top organic layer was retained, dried with N_2, and stored at -20°C until analysis. Nomenclature A:Bn-C as defined in Budge (1999) was used to describe PLFAs, where A represents the number of carbon atoms in a given PLFA, B refers to the number of double bonds, and C the position of the double bond closest to the terminal methyl group. A bacterial acid methyl ester mix (BAME, Sigma-Aldrich, batch number BCBT4956) was used to identify PLFAs in samples. The BAME mix was analyzed using a GC-IRMS to identify peaks. Both BAME mix and extracted samples were run on a GC-IRMS to identify (using BAME mix) and quantify (using 19:0 FA standard) peaks and determine $\delta^{13}C$ values of PLFAs. For ease, PLFA were labeled with numbers referring to their sequence in the chromatograms (Table 1.1).

Concentrations for each bacterial PLFA per gram of sediment in microcosm experiments were calculated as follows:

$$\text{PLFA } \left(\frac{\mu g}{mL}\right) = \frac{\left(\frac{19{:}0 \text{ concentration}}{19{:}0 \text{ peak area}} * \text{PLFA peak area}\right)}{\text{dry weight sediment (g)}}$$

where, 19:0 concentration is the concentration of the internal standard added to each sample (230 µg/mL), and dry weight sediment referring to the total amount of freeze-dried sediment used for PLFA extraction in grams. Significant differences in total PLFA concentration between temperature treatments were determined using t-tests (labeled and non-labeled trials combined for n=2 per temperature treatment, significance level $\alpha = 0.05$). In addition, isotope tracer assimilation into each bacterial PLFA over time was determined using a stable isotope mixing model (McMahon et al., 2006; Weems et al., 2012) as follows:

$$X_{tracer}(\%) = \left[\frac{\delta^{13}C_{sample} - \delta^{13}C_{initial}}{\delta^{13}C_{algal\ tracer} - \delta^{13}C_{initial}} \right] * 100$$

where, X_{tracer} refers to the fraction (%) of the tracer incorporated into bacterial PLFA, $\delta^{13}C_{sample}$ being the $\delta^{13}C$ value of the PLFA at the time of sampling, $\delta^{13}C_{initial}$ is the initial $\delta^{13}C$ value of PLFA at t_0, and $\delta^{13}C_{algal\ tracer}$ is the mean labeled algal $\delta^{13}C$ value.

1.3.4 Statistical analysis

To account for the addition and fractionation of carbon during the AA derivatization process, correction factors for each AA were calculated from known reference values for $\delta^{13}C$ of pure amino acids according to O'Brien et al., (2002). Corrected amino acid $\delta^{13}C$ values were normalized for each sample to their respective mean $\delta^{13}C$ ($\delta^{13}C_{EAA} = \delta^{13}C_{EAA} - \text{mean } \delta^{13}C_{EAA}$) to create $\delta^{13}C_{EAA}$ fingerprints (e.g., Rowe et al., 2019) for each sediment layer and allow for direct comparison of fingerprints among samples.

Endmembers in this study included bacteria, diatoms (representative of phytoplankton), and terrestrial plants. $\delta^{13}C_{EAA}$ values of endmembers were taken from Rowe et al., (2019) for diatoms and terrestrial plants, while bacterial $\delta^{13}C_{EAA}$ were used from Larsen et al., (2013). A linear discriminant analysis (LDA, R package "MASS") was applied to test the prediction strength of the association of unknown samples based on $\delta^{13}C_{EAA}$ values of endmember groups. A Shapiro-Wilks test and Box's M test were applied to test for normality and homogeneity of variance, respectively. For this, a randomly selected subset of endmember $\delta^{13}C_{EAA}$ values was eliminated from the original data set and run as unknown samples. Then, endmember $\delta^{13}C_{EAA}$ values were used as predictors to test association of sediment $\delta^{13}C_{EAA}$ values with the various endmember groups. A stable isotope mixing model in R (SIMMR, https://cran.r-project.org/web/packages/simmr/vignettes/simmr.htmL) was used to determine proportional contribution of EAA carbon from the various endmembers to sediments. Proportional (%) EAA carbon contributions of endmembers were determined for each sediment depth section at each station (the upper two sediment layers (0-2 cm) were averaged to account for sampling biases). Here, we used EAA source contribution as a proxy for overall carbon contribution to sediments.

Most statistical analyses were performed in R using the RStudio interface version 1.1.383. Prior to parametric statistical analyses, normality of data was tested using a Shapiro-Wilks test, homogeneity of variance using Levene's test, and independence using a chi-squared test. Data were transformed, if necessary, in the following order: square root, cube root, and log transformation until assumptions were met. Significant differences in proportional contributions of each endmember among sediment depth

layers, and differences in proportional contributions among endmembers within each sediment depth layer (stations used as replicates for both analyses) were determined using analyses of variance (ANOVA) with Tukey's honest significant difference post-hoc test at a significance level of $\alpha = 0.05$. A BEST analysis (PRIMER version 7.0.13) determined relationships among average proportional carbon contributions of all endmember groups in surface sediments (0-2 cm layer) and environmental variables: bottom temperature, bottom salinity, sediment grain size, sediment chlorophyll *a* content, total organic carbon (TOC), bulk sediment C/N ratios, and $\delta^{13}C$ and $\delta^{15}N$ values.

1.4 Results

Normalized $\delta^{13}C_{AA}$ values of each sediment layer were averaged across stations for each EAA, and overall fingerprints were very consistent among depth layers (Fig. 1.2). The LDA predictor strength of randomly chosen endmember $\delta^{13}C_{AA}$ values showed that >65 % were predicted accurately. Proportional contributions of EAA from the three endmember groups to sediment samples from SIMMR calculations were highly variable. On average, bacteria contributed 31.0 % (5.7 – 50.1 %), while phytoplankton averaged 30.1 % (9.9 – 64.9 %). Terrestrial carbon contributions (3.8 – 80.6 %) made up the highest average carbon contribution with 38.8 %. Spatial distribution of average proportional carbon contributions in the 0-2 cm sediment layer did not reveal a clear pattern across the shelf although terrestrial contribution was especially high at the two mid-shelf stations in the southern Chukchi Sea (Fig. 1.3). Accordingly, there was no significant relationship between proportional carbon contributions and environmental variables (highest correlation with sediment $\delta^{13}C$, rho = 0.045, BEST analysis). No significant differences in the proportional contributions of terrestrial and bacterial EAA among sediment layers was identified ($p>0.05$, ANOVA, Fig. 1.4). Only phytoplankton contributions were significantly different between the top layer (0-2 cm) and bottom layer (4-5 cm) ($p = 0.04$, ANOVA). Proportional contributions of terrestrial carbon in the 2-3 cm and 3-4 cm depth sediment layers were significantly higher compared to other carbon sources and significantly higher compared to phytoplankton in the 4-5 cm depth layer ($p = 0.03$, ANOVA) (Fig. 1.5).

Total PLFA concentrations in microcosm experiments between the 0°C and 5°C treatment (combining labeled and non-labeled trials for each temperature treatment) were significantly different when tested for overall difference ($p = 0.02$, t-test) (Fig. 1.6). Total PLFA concentrations over time were noticeably higher in the 5°C treatment at 12 and 24 h, but given the low number of replicates (n=2) only the difference at 24 h was significant ($p = 0.01$, t-test). The differences between the temperature treatments seemed to be driven by overall higher concentrations of the individual PLFAs tested at 5°C;

however, specifically methyl-cis-9-hexadecanoate (C 16:1 cis-9, PLFA 14) and methyl-heptadecanoate (C 17:0, PLFA 18) were higher at the 5°C treatment at 12 h and 24 h (Fig. 1.7, see Table 1.1 for PLFA numbers).

Only five PLFAs showed incorporation of isotopically labeled material, indicated by changes in individual PLFA $\delta^{13}C$ values of up to 500 ‰ throughout the experiment (Fig. 1.8). Other PLFAs only showed marginal changes in the PLFA $\delta^{13}C$ values of ±15 ‰ and were not included in carbon incorporation analyses. The proportional contribution of carbon incorporated into these five PLFAs from labeled algal material seemed to be higher in the 5°C treatment compared to the 0°C treatment. The PLFA showing highest incorporation of labeled material was methyl-cis-9-hexadecanoate (PLFA 14) with proportions of carbon incorporation ranging from 0.16 – 33.56 %. PLFA 10 (methyl-pentadecanoate, 0.96 – 11.00 %), PLFA 20 (methyl-linoleate, 0.19 – 11.41 %), PLFA 21 (methyl-oleate, 0.65 – 4.35 %) and PLFA 22 (methyl-trans-9-octadecanoate, 0.95 – 8.03 %) only showed small carbon portions to be derived from labeled material.

1.5 Discussion

The unprecedented climate-induced changes occurring in the Arctic Ocean have the potential to influence the composition of organic matter sources in Chukchi Sea shelf sediments that are essential in carbon cycling and contribute to the base of the benthic food web. The goal of this study was to identify the proportional contributions of carbon sources in *in situ* sediments across the Chukchi Sea and within the top 5 cm sediment horizon. Overall, results revealed no clear spatial pattern of the three main carbon sources (phytoplankton, terrestrial, and bacterial) across the shelf in relation to environmental variables, and carbon sources in sediments were relatively well-mixed over the top 5 cm. Phytoplankton contribution slightly decreased in deeper sediment layers and terrestrial matter was present in significantly higher proportions in deeper sediment depths (>2 cm) compared with other sources. Increased bacterial production at higher experimental temperatures indicated a potential increase in the proportion of bacterial carbon in a future, warmer Arctic.

A method that can reliably distinguish among different sources is essential to the goal of determining biosynthetic sources contributing organic carbon to sediments. Biomarker approaches have been commonly applied to distinguish multiple sources in benthic food webs from the Arctic, employing bulk stable isotope analysis (e.g., Iken et al., 2010; Divine et al., 2015; Bell et al., 2016; McTigue and Dunton, 2017; Harris et al., 2018) or fatty acid analysis (Schollmeier et al., 2018), or a combination of the two to distinguish sea ice and phytoplankton production and separating terrestrial from marine sources

(Budge et al., 2007; Oxtoby et al., 2016; Oxtoby et al., 2017; Paar et al., 2019). Using EAA stable isotope fingerprinting allowed us to complement these other biomarker methods and address some of the limitations of other approaches (Post, 2002; Close, 2019). EAA stable isotope fingerprinting shows only marginal variations among phylogenetically close groups (i.e., carbon source endmembers) (Larsen et al., 2013; Larsen et al., 2015), making it a more specific biomarker approach. Although the fingerprinting method is a powerful tool to trace carbon sources, the analysis of proportional contributions using mixing models is dependent on the source information supplied. For example, predictions of endmember contributions will only include those sources supplied to the model. Conversely, every endmember that is supplied to the model will always result in the assignment of at least some proportional contribution (Phillips et al., 2014). Here, we included marine phytoplankton, terrestrial matter, and bacterial carbon as sources and excluded macroalgal carbon that has been included in other studies (Larsen et al., 2013; Larsen et al., 2015; McMahon et al., 2016). Macroalgae are uncommon along the Chukchi Sea coast (Mohr et al., 1957; Wulff et al., 2009), and while the occasional drift of algal material offshore cannot be excluded, it is unlikely to be a common carbon subsidy into Chukchi shelf sediments. In addition, the potentially high biomass and important role of fungi in the degradation of organic matter is increasingly acknowledged (Raghukumar, 2017), but isolating and characterizing this endmember as a source is currently outside our ability. In addition, mixing models provided relative contributions of EAA and not absolute concentrations of carbon sources to a given sample. Hence, results will need to be interpreted within the framework of such potential limitations, but our ecological knowledge of the system allowed us to select the most likely sources, and results will be especially valuable in assessing potential shifts in relative sources in the future.

Relative contributions of different EAA sources to sediments did not display a clear spatial pattern across the shelf and did not correlate with any environmental variables tested. The Chukchi Sea is characterized by distinct water masses of different temperature, salinity, and nutrient content, influencing the respective productivity regimes (Walsh et al., 1989). However, all sampling sites for this study were located within the salty, cold, nutrient-rich, and highly productive Bering Shelf Anadyr Water (BSAW), based on bottom temperature and salinity data taken during the cruise. Also, all sampling locations were similar in their depth range. Similar productivity regimes for all stations based on their water mass designation may in part explain the similarity of EAA sources across all sites. Although, water mass may not be the sole potential predictor of sediment EAAs. For example, flow regimes can differ within a water mass and are a driving force in the formation of local environmental conditions, e.g., grain size, TOC content, and the deposition of suspended material. Current velocities on the Chukchi shelf often

exceed 1.0 m s^{-1} during strong local storms (Weingartner et al., 1998), and they vary depending on topography (Winsor and Chapman, 2004), season (Woodgate et al., 2005), remote atmospheric forcing (Danielson et al., 2014), and the shelf density field (e.g., (Weingartner et al., 2017). Regions with lower flow variance are usually associated with smaller sediment grain size and higher deposition of organic matter, as the weaker currents allow smaller particle sizes to settle out of the water column, while strongly advective regions with swifter currents are characterized by coarser sediments and less organic matter deposition (Blanchard et al., 2013; Pisareva et al., 2015). While it is possible that flow velocities influence local environmental conditions, the absence of a spatial pattern in EAA contributions in sediments indicate that relative proportions of different EAA sources across the shelf are largely unaffected by these flow conditions.

We observed high contributions of terrestrial EAA at the two southern-most offshore stations in Hope Basin, north of the Bering Strait; however, no overall large-scale patterns in EAA contributions were detected. Within the spatial and temporal variability of the overall depositional shelf of the Chukchi Sea (de Haas et al., 2002; Lepore et al., 2007), the Hope Basin in the south-central Chukchi Sea is known regionally for the especially high deposition rates of organic matter, supporting rich "hotspots" of macrofaunal communities (Grebmeier et al., 2015). Terrestrial matter that is partially degraded during oceanic transport tends to associate with lithogenic particles, which increases their settlement in these high depositional regions (Mayer, 1994). Terrestrial matter in the Chukchi Sea mostly derives from the Anadyr River in Siberia and the Yukon River in Alaska (Li et al., 2017) with smaller contributions of the Kobuk and Noatak rivers in Kotzebue Sound (McManus and Smyth, 1970; McManus et al., 1974; Naidu et al., 1982). For example, the Yukon River alone discharges $2.02 \cdot 10^{12}$ g TOC annually into the ocean (Guo and Macdonald, 2006). Sea ice can be a significant vector in the distribution of terrestrial matter beyond the coastal region farther onto the shelf and even into the deep basin in the Arctic (Yunker et al., 2005). Ocean currents slow north of the high-flow constriction presented by the Bering Strait, likely allowing for increased deposition of terrestrial matter in the Hope Basin region (Li et al., 2017). This could explain the observed higher proportional contribution of terrestrial EAA in sediments in this region relative to the stations farther north and regions of swifter currents found closer to the Alaskan coast (e.g., Clement et al., 2005).

EAA contributions of the three endmember sources across the top 5 cm sediment layers were relatively even, and no significant depth-related trends for any source were found except for a slight decrease in phytoplankton proportion with increasing sediment depth. Commonly, chlorophyll *a* and POC

concentrations show an exponential decrease with sediment depth and these concentration gradients are dependent on both the transport and decomposition of this material within the sediment (Sun et al., 1991; Sun et al., 1994). Marine microalgae (phytoplankton and ice algae) are a labile organic matter source and material deposited onto the seafloor is quickly consumed at the sediment surface by benthic consumers (Sun et al., 2007). The most labile dissolved organic portions of microalgal matter, such as lipids, are also biodegraded within days by bacteria (Newell et al., 1981; Canuel and Martens, 1996). Bioturbation from feeding activity of marine invertebrates can result in a drawdown of the remaining particulate microalgal fractions into deeper sediment layers, although this drawdown likely diminishes in deeper sediment layers, except in the presence of benthic feeding marine mammals in which case bioturbation depth is highly increased (Ray et al., 2006; Kristensen et al., 2012). The Chukchi Shelf, including the locations of sediment collections for this study, are characterized by high benthic invertebrate biomass with a variety of feeding types that contribute to bioturbation (Iken et al., 2010; Iken et al., 2019). While the subducted particulate fractions of phytoplankton are typically more refractory and have degradation times on the order of weeks to months (Newell et al., 1981; Garber, 1984; Kristensen and Holmer, 2001), the observed decrease in phytoplankton EAA proportions with depth could be a result of degradation rates in deeper layers exceeding the amount of particle transport from surface sediment down to depth (Sun et al., 1994). Hence, high deposition of microalgae onto the sediment surface, combined with some subduction from bioturbation and continued degradation within the sediments, can cause the depth-related gradient in relative proportions of phytoplankton we hypothesized and observed.

Contrary to our hypothesis, the proportional contributions of bacterially-derived EAA showed no change with sediment depth. This is in contrast to studies conducted elsewhere (e.g., Mediterranean Sea), where bacterial biomass decreased with sediment depth because of a decline in concentration of labile compounds and relative increase of less degradable, more refractory compounds less prone to bacterial degradation (Fabiano and Danovaro, 1994). Conversely, others have suggested that deeper, paleo-sedimentary archives can contain higher proportions of bacterial carbon compared to other carbon sources based on EAA fingerprinting (Larsen et al., 2015). Bioturbation that subducts organic matter into deeper sediment layers also enhances ventilation rates within the sediment, which influence physical, chemical and biological properties within the deeper sediments (Mermillod-Blondin et al., 2004; Kristensen et al., 2012; North et al., 2014). For example, degradation processes are dependent on the availability of electron acceptors, which are directly influenced by processes such as bioturbation and can govern the type of diagenetic process occurring with depth (Nealson, 1997; Fenchel, 2008). The increased O_2 penetration into sediment depths from bioturbation (Kristensen and Holmer, 2001; Mermillod-Blondin

and Rosenberg, 2006) supports bacterial degradation of labile matter within the bioirrigated layer (Hulthe et al., 1998; Kristensen et al., 2012). O_2 penetration also increases the typically slow, thermodynamically limited anaerobic degradation rates of refractory matter buried in these deeper sediment layers (Hulthe et al., 1998; LaRowe and Van Cappellen, 2011). Despite O_2 availability, the buildup of bacterial carbon is highly reliant on the amount and specific lability of the buried material (Legendre and Le Fevre, 1995; Pomeroy and Wiebe, 2001). A "priming" effect has been suggested for labile organic matter in deeper layers, where either the breakdown of this labile matter stimulates the production of extracellular enzymes that are active in degrading the more refractory material, or where the labile matter provides energy for a bacterial community that is then able to degrade the refractory matter (van Nugteren et al., 2009). Bacteria can assimilate available carbon in a matter of hours (Moodley et al., 2000), and cell lysis of dead bacterial cells releases nutrients and substrate that living bacteria are able to utilize to maintain bacterial community biomass. These processes may cause relatively constant bacterial degradation and production in all sediment depths and, therefore, the observed consistent bacterial EAA contribution across sediment depths.

Terrestrial EAA contributions also were relatively consistent over sediment depth horizons, and were present in significantly higher proportions compared with the other two sources in sediment depths >2 cm. This is consistent with findings from Svalbard fjords, which showed higher amounts of lighter carbon isotope bulk organic material in sediments >1 cm, which was attributed to increases in terrestrial matter (Koziorowska et al., 2016). The initial, and rate-limiting, step of bacterial degradation of organic matter is the extracellular enzymatic hydrolysis of the high-molecular-weight organic matter such as in terrestrial matter (Arnosti et al., 1998; Arndt et al., 2013). Terrestrial matter contains a high amount of structurally highly complex components, e.g., macromolecules like lignin and cellulose, and other molecules with high numbers of double bonds (Hedges et al., 1997; Opsahl and Benner, 1997; Baldock et al., 2004; Garneau et al., 2009). While this typically renders terrestrial material as less labile than marine-derived matter, overall degradability of terrestrial matter also differs depending on its age. Ancient terrestrial carbon is highly recalcitrant, while modern material is somewhat more labile (Goñi et al., 2005; Kim et al., 2011). During the transport from shore onto the shelf, much of the labile fraction of terrestrial matter is already subject to degradation, increasing the refractory proportion of the residual material when finally deposited onto the seafloor (Canuel and Martens, 1996; Lee et al., 2004). Hydrolysis rates in subsurface sediments can actually be higher than in surface sediments, but efficiency ultimately depends on how recalcitrant the material is (Teske et al., 2011). The remaining refractory portion of terrestrial matter after initial degradation in the water column and ancient carbon, which can make up the majority

of total terrestrial carbon influx from Arctic rivers (Goñi et al., 2005), could have long degradation times, leading to accumulation in the deeper sediments (Canuel and Martens, 1996). These processes fit well with a higher proportion of the organic matter at these deeper layers being of terrestrial origin.

The relatively high proportions of terrestrial EAA found in Chukchi Sea sediments are not unusual for Arctic sediments. Most terrestrial matter comes from discharge of large Arctic rivers as well as groundwater seepage (McClelland et al., 2006). Permafrost and its accelerated melting due to climate warming also contribute substantial amounts of terrestrial matter to river discharge (Guo et al., 2007; Loiko et al., 2017). Terrestrial matter contributed 70 % (Winkelmann and Knies, 2005) and up to 80 % (Koziorowska et al., 2016) to the bulk organic carbon in fjords in the European Arctic, based on sediment bulk stable isotope analyses. While comparability of studies based on different methodology is limited, our values of about 50 % terrestrial matter of the EAA sources are lower than those for overall carbon sources from fjord environments, but suggest that our values are likely not overestimated and that terrestrial contributions to sedimentary carbon exceeding those from marine phytoplankton is common. The higher percentage values from the fjord systems likely derive from higher glacial input in such systems (Winkelmann and Knies, 2005; Koziorowska et al., 2016).

Bacterial activity in degradation processes is not only dependent on the degradability of the organic matter but also on temperature. While polar bacteria are physiologically well adapted with high specific metabolic rates that support activity at low *in situ* temperatures (Arnosti et al., 1998; Knoblauch et al., 1999), their activity is sensitive to increases in water temperature. In fact, metabolic rates increase at optimal temperatures that are typically above *in situ* temperatures in polar systems (Rysgaard et al., 2004; Kirchman et al., 2005; Kirchman et al., 2009; Robador et al., 2009). As hypothesized, our microcosm experiment showed increased bacterial production, although intermittent, at the higher temperature (5°C). This is similar to another Arctic study that found a six-fold increase in bacterial production at incubations 6°C above ambient conditions (Kritzberg et al., 2010). Thus, despite physiological adaptations to low temperatures, optimal growth rates are not achieved *in situ* in Arctic bacteria and, bacterial community activity is lower compared to those in temperate regions (Pomeroy and Deibel, 1986; Middelboe and Lundsgaard, 2003; Kirchman et al., 2005; Kirchman et al., 2009). Higher bacterial production at higher temperatures has been attributed to increased substrate affinity of extracellular enzymes at warmer temperatures as well as increased substrate assimilation within the cell (Nedwell, 1999). As substrate availability was equal across both temperature treatments in our incubation study, the increase in sediment bacterial production between treatments is attributable to temperature effects.

This is similar to global (López-Urrutia and Morán, 2007) and Arctic (Kritzberg et al., 2010) studies that found clear increases in bacteria production in response to higher temperature if resource availability was equal.

Higher temperature treatment (5°C) resulted in higher bacterial community productivity, which peaked at 12-24 h, after which PLFA concentrations started to level with those of the 0°C treatment. In comparison, the 0°C treatment showed no changes in PLFA production over the course of the experiment. The decrease in overall PLFA concentration after 24 h in the 5°C treatment could have multiple reasons. Firstly, the production of bacterial PLFAs is indicative of bacterial biomass and is dependent on the availability of substrate (Thingstad et al., 2002). Secondly, the substrate may become rapidly depleted in sediment incubations experiments that are not supplied with any additional nutrients, resulting in a rapid decrease in overall activity of the bacterial community within hours (Novitsky and Morita, 1977; Goldman et al., 1987; Lopez et al., 1998). For our experiment, no additional substrate was provided throughout the incubation period past the original addition, likely leading to an increase in bacterial production from the higher rates supported by high temperatures. Once labile substrate was drawn down, resources were too limited to support the higher bacterial production rates at 5°C. A similar decline in bacterial production was not observed at the 0°C treatment, possibly because the lower production rates had not yet led to substrate limitation. Finally, increased predation of bacteria by flagellates or meiofauna and viral lysis (Almeida et al., 2001) could contribute to the decrease in PLFA concentration after 12-24 h at higher temperatures.

Changes in PLFA concentrations between the temperature treatments seemed to be largely driven by two PLFAs: methyl-cis-9-hexadecanoate (PLFA 14) and methyl-heptadecanoate (PLFA 18). PLFA 14 is produced by both Gram-positive and Gram-negative bacteria, while PLFA 18 is usually produced only by Gram-positive bacteria (Kaur et al., 2005). Although PLFA analysis is a widely applied tool enabling us to trace the fate of specific substances, such as methane and contaminants through bacterial communities (Kaplan and Bott, 1989; Evershed et al., 2006; He et al., 2015), the use of PLFAs as a biomarker for taxonomic resolution of the bacterial community is still debated (Ruess and Chamberlain, 2010; Frostegård et al., 2011). A good biomarker is defined by being highly source specific; however, while some PLFAs are assigned to specific groups of bacteria, they often are produced by multiple groups of bacteria, making taxonomic distinction of the bacterial community based on PLFA patterns difficult (Frostegård et al., 2011; Yao et al., 2014). Higher taxonomic resolution, such as from DNA-stable isotope probing (Radajewski et al., 2000), is needed to make detailed inferences about the specific groups of bacteria

responsible for the differences observed. Although taxonomic resolution is coarse, overall PLFA presence and concentrations showed high overlap between the 5°C and 0°C treatments, indicating that differences in production but no major changes in community composition occurred.

Only five out of eleven PLFAs showed isotopic label incorporation from substrate throughout the incubation period (Table 1.2). Incorporation of labeled material into newly formed PLFAs seemed to be slightly higher in the 5°C treatment, although only a small fraction (0.16 – 33.56 %) of isotopically labeled carbon was incorporated during PLFA synthesis. This supports findings in previous studies of only marginal assimilation of labeled substrate into bacterial PLFAs (Boschker et al., 1998; Moore-Kucera and Dick, 2008). Labeled material is slightly higher in molecular weight and, therefore, may not be taken up preferentially and incorporated into all PLFA by bacteria (Cifuentes and Salata, 2001). The incorporation of only small fraction of labeled PLFAs indicates that the majority of the bacterial community is carbon derived from other carbon substrates than the provided microalgae. These probably included organic matter and dissolved organic carbon (DOC) present in the sediment, porewater and water supplied to the experimental set up, as well DOC released from predation and viral lysis of bacteria (Qiu et al., 2009) or internal carbon turnover in bacterial cells.

In conclusion, carbon sources in Chukchi Sea sediments were relatively well-mixed over the top 5 cm horizon with large proportions of terrestrial carbon. Sediment bacterial production showed initial increases at higher temperatures but then decreased, likely due to substrate limitations or an increase in predation activity and viral lysis. The effects of climate-driven changes in temperature are likely to be especially prominent on Arctic shelves. Resulting changes in the strength of pelagic-benthic coupling and increases in riverine input have the potential to shift the composition of carbon sources in Arctic sediments. Additionally, temperatures higher than current *in situ* conditions increase bacterial metabolism and production in sediments, indicating a potential increase in this bacterial carbon source in a future, warmer Arctic. These potential shifts in carbon source contributions to the sediments could have strong implications for carbon storage or mobilization in sediments and the carbon flow through the Chukchi sea benthic food web.

1.6 Acknowledgments

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1.7 Figures and tables

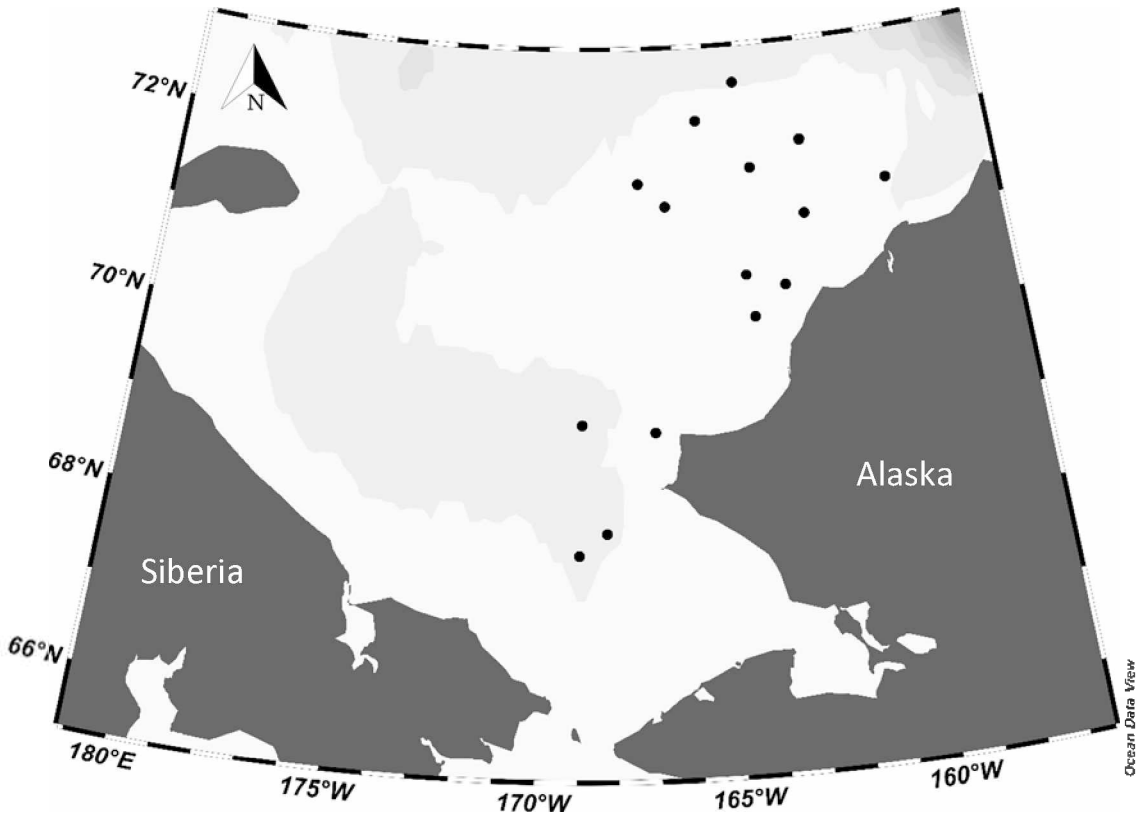

Figure 1.1: Chukchi Sea stations (black dots) sampled for sediment during the AMBON 2015 cruise. Darker gray shade indicates the 50 m isobath on the Chukchi Shelf.

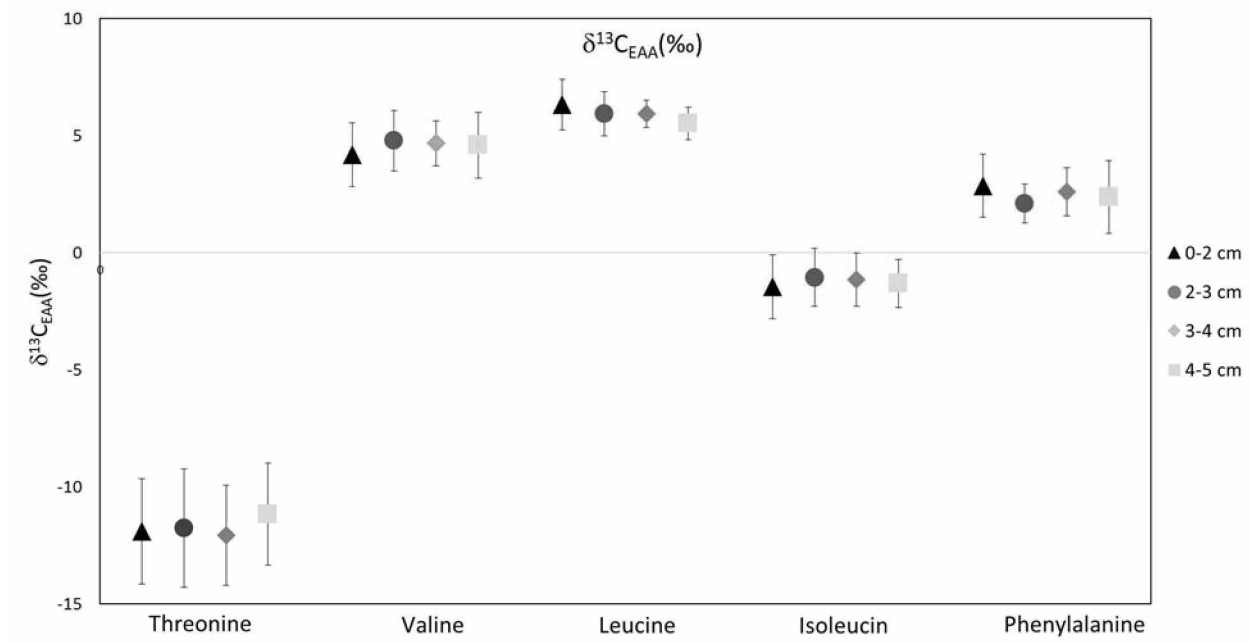

Figure 1.2: $\delta^{13}C$ values of essential amino acids averaged for each Chukchi Shelf sediment depth layer across all stations.

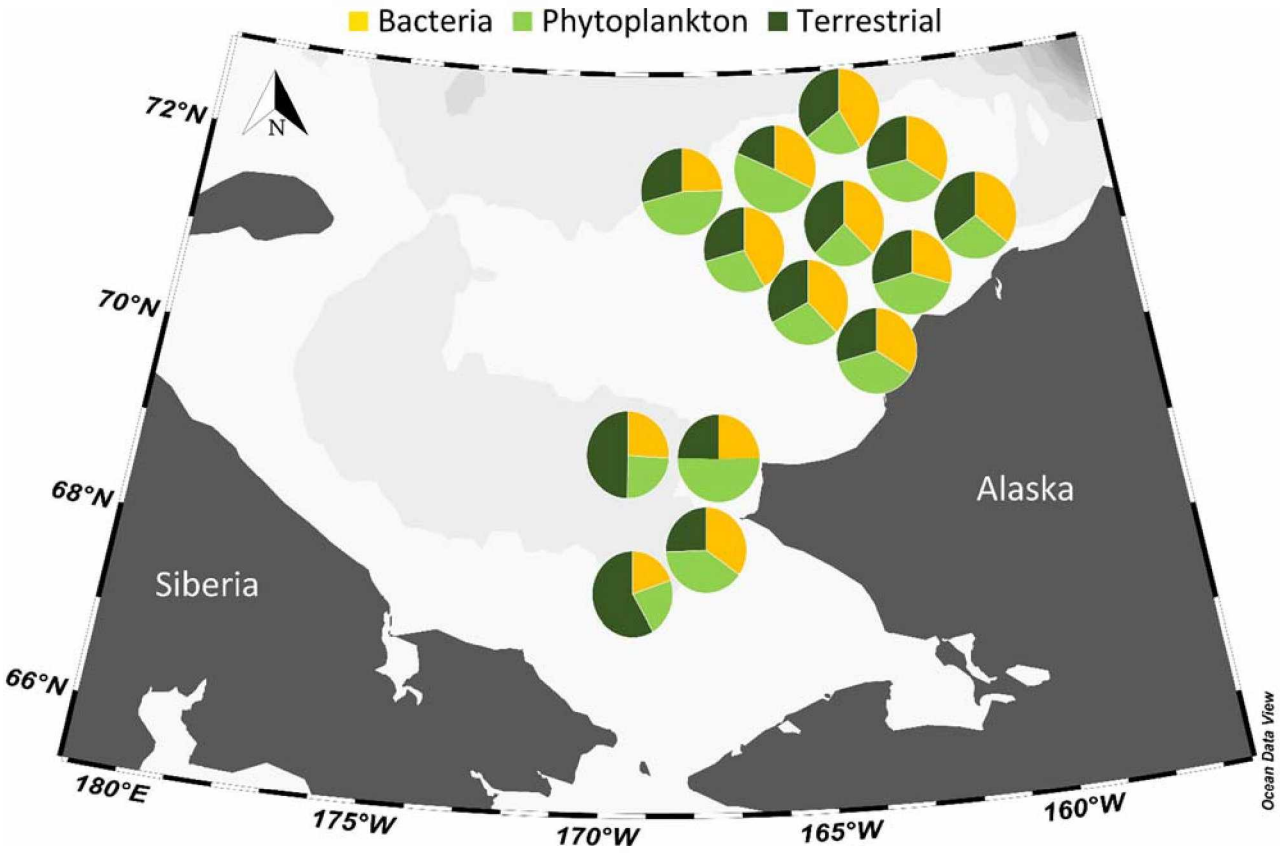

Figure 1.3: Mean proportional contributions (%) of three essential amino acid sources (bacteria, phytoplankton, terrestrial) for the 0-2 cm sediment layer across the Chukchi Sea Shelf.

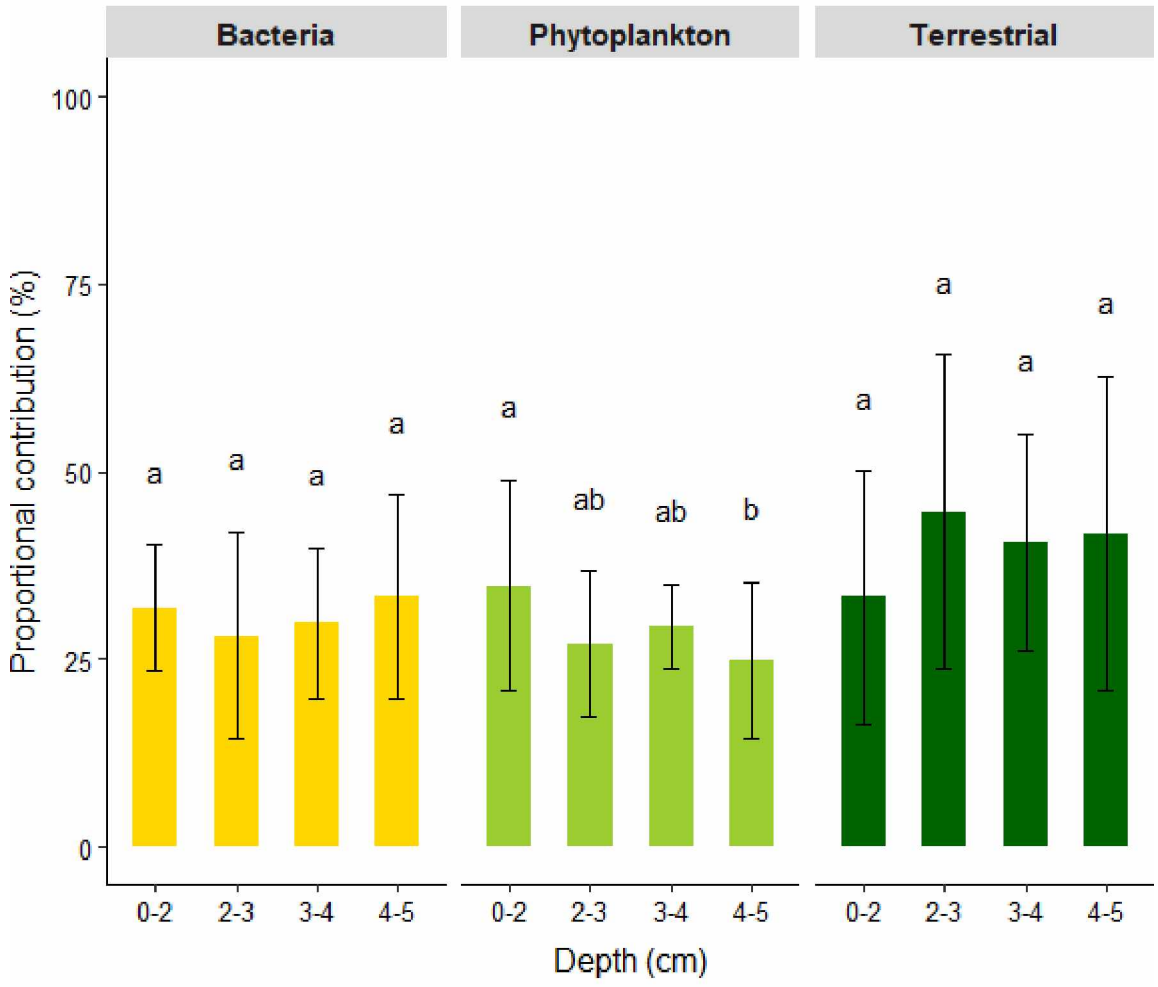

Figure 1.4: Mean proportional contributions (%, mean ± 1 SD) of three essential amino acid sources (bacteria, phytoplankton, and terrestrial) for each Chukchi Shelf sediment depth interval (cm). Letters above bars indicate significantly ($p<0.05$) different contributions within each source among depth layers (n=14 per sediment layer).

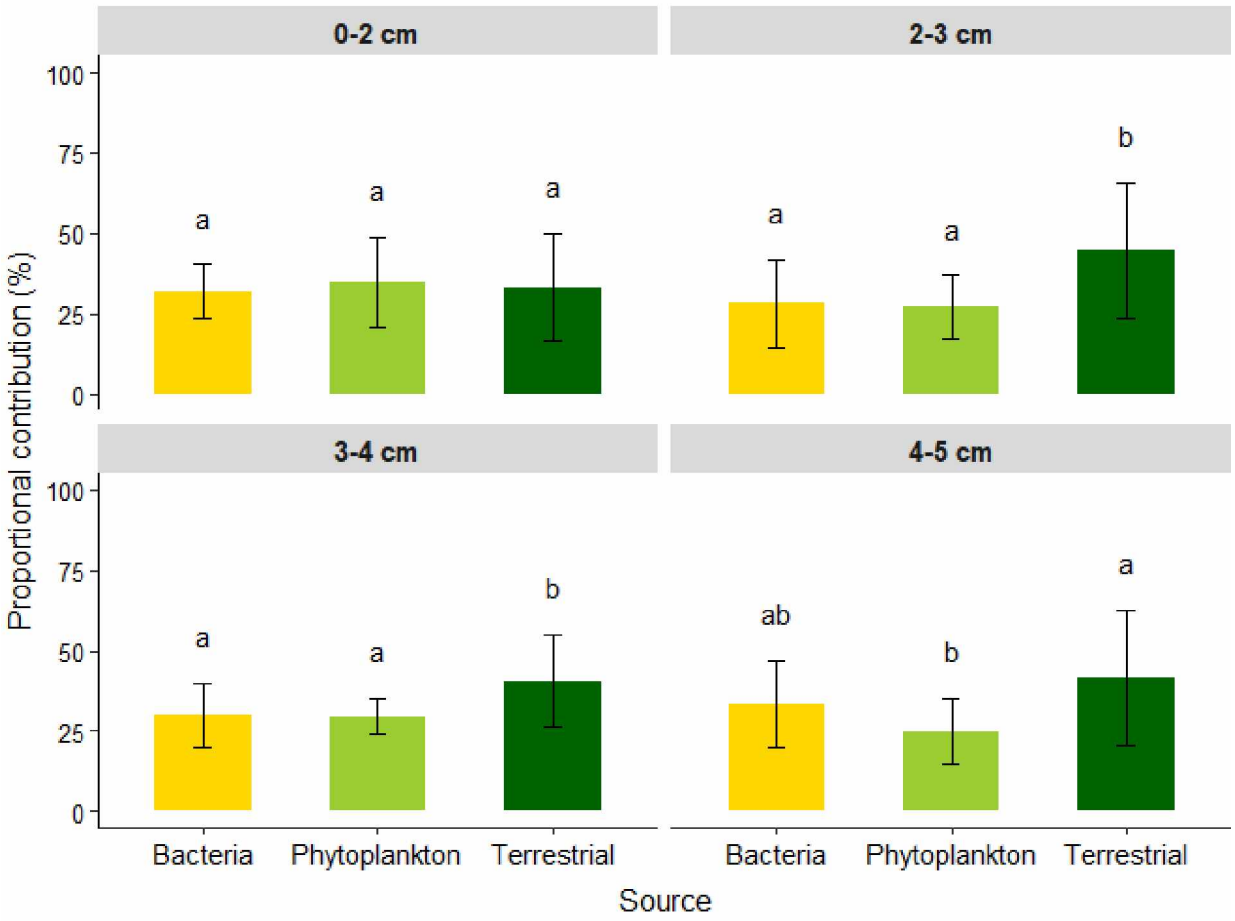

Figure 1.5: Mean proportional contributions (%, mean ± 1 SD) of the three essential amino acid sources (bacteria, phytoplankton, and terrestrial) within Chukchi Shelf sediment depth intervals (cm). Letters above bars indicate significantly ($p<0.05$) different contributions among sources within each sediment depth layer (n=14 per sediment layer and source).

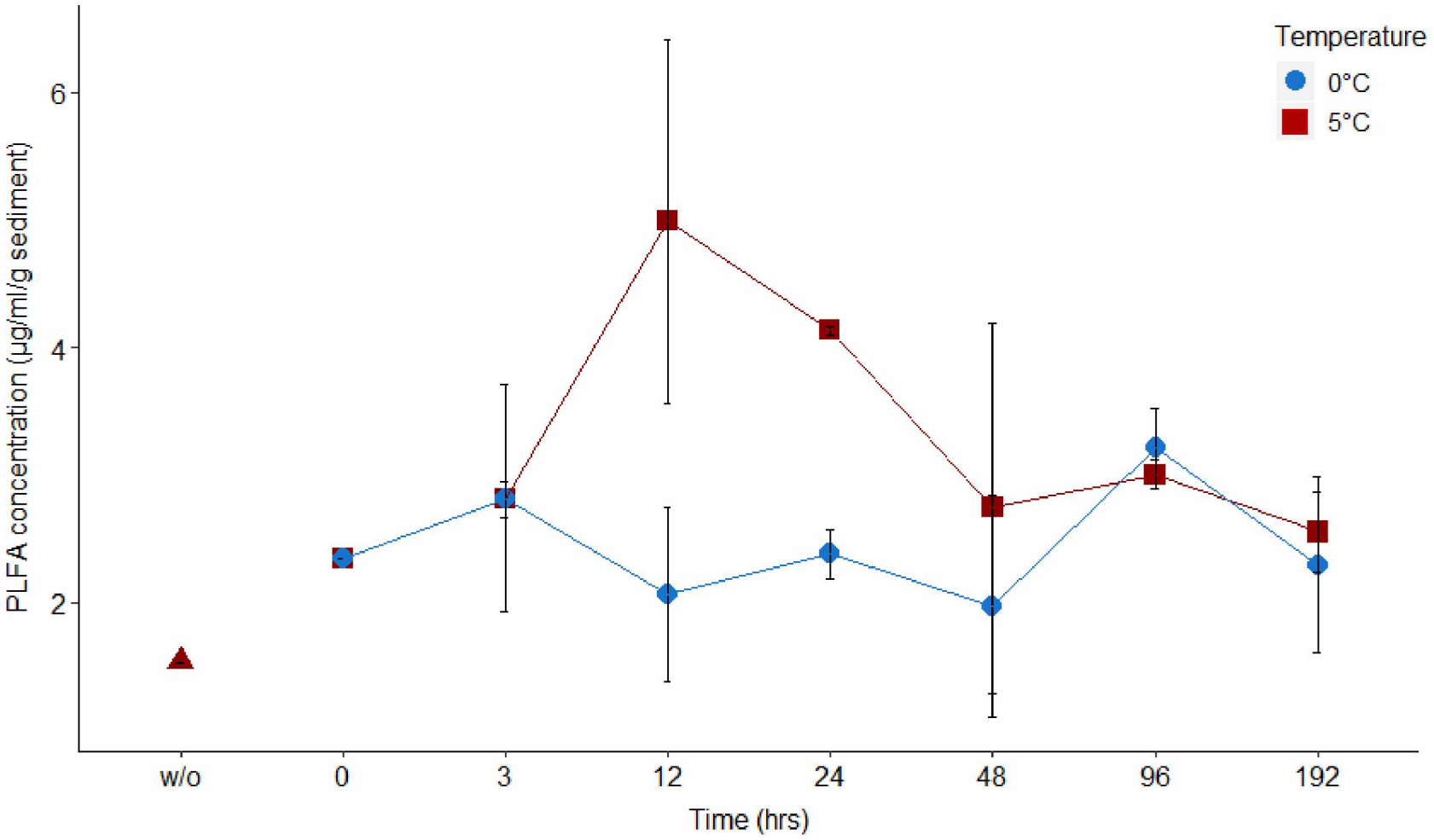

Figure 1.6: Total phospholipid fatty acid (PLFA) concentration in marine sediments over 192 h for two temperature treatments, 0°C (light gray, circle) and 5°C (dark gray, square) (mean ± 1 SD, n=2 per treatment and time, except at T_0 and w/o). Time point w/o (triangle) indicates the sediment sample without addition of algae at time 0 h.

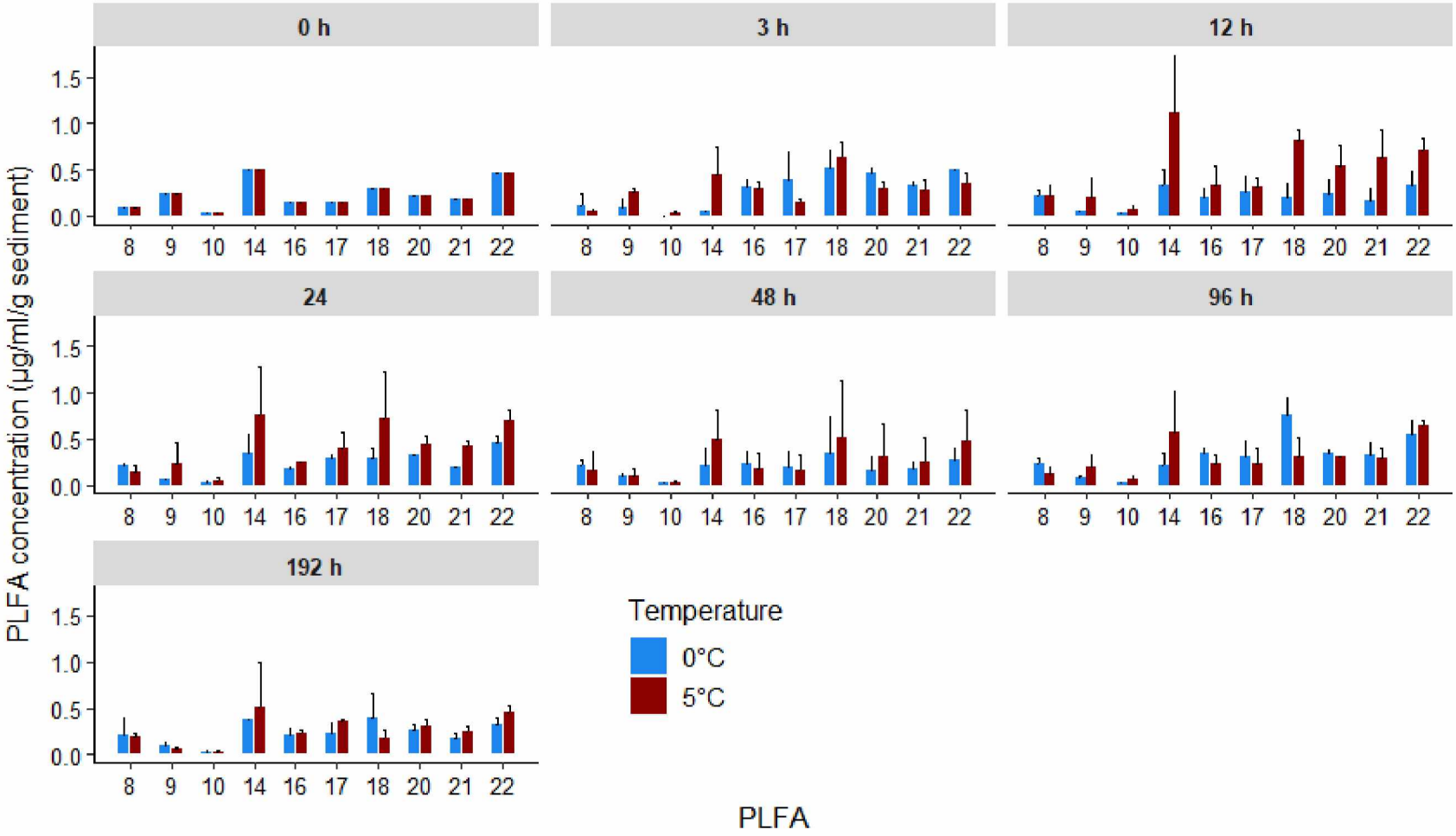

Figure 1.7: Phospholipid fatty acid (PLFA) concentrations in marine sediments over 192 h (time given in bars above graphs) at two temperature treatments (mean ± 1 SD, n=2 per treatment and time, except at T_0), 0°C (light gray) and 5°C (black). PLFA numbers relate to PLFA identity (see Table 1.1).

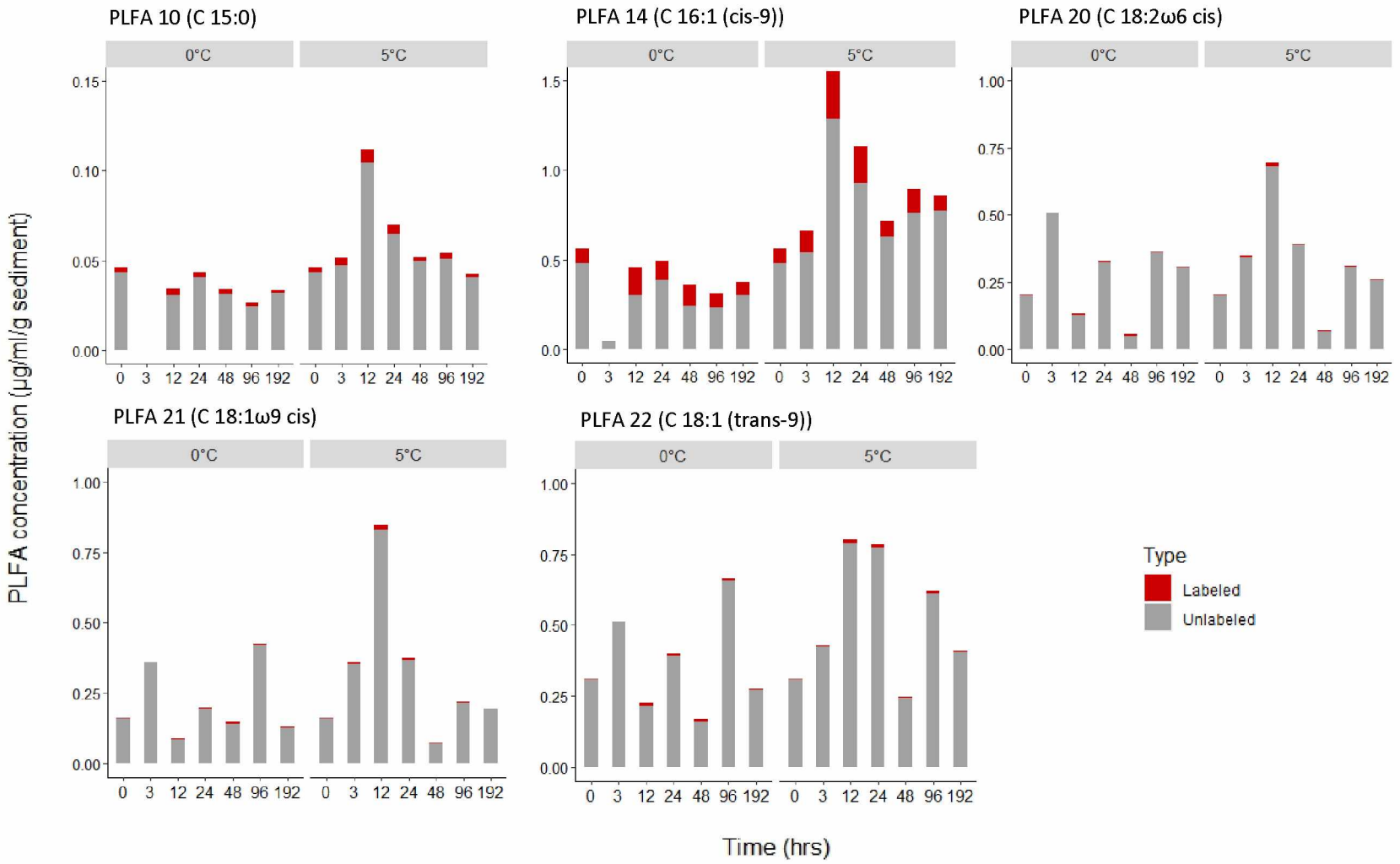

Figure 1.8: Isotopically labeled (^{13}C, black) and unlabeled (gray) portion of phospholipid fatty acid (PLFA) concentrations in marine sediments over time (h) at two temperature treatments (0°C and 5°C, n=1 per treatment) for selected PLFA.

Table 1.1: List of phospholipid fatty acid (PLFAs) detected in microcosm marine sediment samples, respective PLFA numbers and their source affiliations. Fatty acid nomenclature e.g., 18:2n6 refer to the number of carbon atoms (18), number of double bonds (2), and position of first double bond.

PLFA #	PLFA name	Nomenclature	Source
7	Methyl-myristate	C 14:0	Eukaryotes & Prokaryotes
8	Methyl-13-methyltetradecanoate	iso- C 15:0	Gram-positive bacteria
9	Methyl-12-methyltetradecanoate	anteiso- C15:0	Gram-positive bacteria
10	Methyl-pentadecanoate	C 15:0	Gram-positive & Gram-negative bacteria
14	Methyl-cis-9-hexadecanoate	C16:1 (cis-9)	Gram-positive & Gram-negative bacteria
15	Methyl-palmitate	C 16:0	Eukaryotes & Prokaryotes
16	Methyl-15-methylhexadecanoate	iso C 17:0	Gram - positive bacteria
17	Methyl-cis-9,10-methylenehexadecanoate	C 17:0 cyclo	Gram - negative bacteria
18	Methyl-heptadecanoate	C 17:0	Bacteria
19	Methyl-2-hydroxyhexadecanoate	2-OH C 16:0	Unknown
20	Methyl-linoleate	C 18:2ω6 cis	Fungi
21	Methyl-oleate	C 18:1ω9 cis	Gram - negative bacteria
22	Methyl-trans-9-octadecanoate	C 18:1 (trans-9)	Gram - negative bacteria
23	Methyl-stearate	C 18:0	Eukaryotes & Prokaryotes
25	nonadecanoate	C 19:0	Standard
26	Methyl-eicosenoate	C 20:0	Eukaryotes & Prokaryotes

Table 1.2: List of overall average (± 1SD) individual phospholipid fatty acid (PLFA) $\delta^{13}C$ values in marine sediments. Gray areas indicate PLFAs chosen for further analysis of incorporation of labeled material into newly formed PLFAs.

PLFA #	Nomenclature	0°C labeled	0°C unlabeled	5°C labeled	5°C unlabeled
8	iso C15:0	-18.0 ± 6.7	-23.5 ± 2.5	-20.8 ± 7.4	-23.5 ± 0.7
9	anteiso C15:0	-11.8 ± 11.5	-23.7 ± 0.7	-14.0 ± 8.8	-25.7 ± 2.4
10	C15:0	149.2 ± 49.8	-20.3 ± 3.6	116.6 ± 34.3	-19.3 ± 3.1
14	C16:1 (cis-9)	466.8 ± 267.0	-22.0 ± 1.4	320.8 ± 77.7	-23.4 ± 1.8
16	iso C17:0	-27.4 ± 2.8	-25.1 ± 1.4	-24.7 ± 1.3	-25.9 ± 0.8
17	C17:0 cyclo	-30.1 ± 4.9	-28.3 ± 2.2	-26.0 ± 3.2	-27.4 ± 1.9
18	C17:0	-23.6 ± 7.7	-26.7 ± 0.6	-25.6 ± 1.3	-26.9 ± 0.9
19	2-OH C16:0	-25.0 ± 4.7	-26.3 ± 1.2	-27.8 ± 3.7	-27.8 ± 2.0
20	C18:2ω6 cis	45.6 ± 93.2	-26.4 ± 1.2	2.2 ± 18.9	-26.9 ± 0.9
21	C18:1ω9 cis	24.1 ± 36.7	-26.1 ± 0.8	30.7 ± 21.4	-26.4 ± 1.2
22	C18:1 (trans-9)	40.9 ± 64.2	-25.0 ± 0.8	11.9 ± 8.7	-25.5 ± 0.6

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Chapter 2: Does feeding type matter? Contribution of organic matter sources to benthic invertebrates on the Arctic Chukchi Sea shelf[2]

2.1 Abstract

Benthic communities play an important role in the nutrient cycling of settling organic matter and provide an energy link to higher trophic levels. These communities are highly dependent on the food sources provided through sinking organic material, with pelagic-benthic coupling particularly strong on Arctic shelf systems. Arctic shelves, however, are experiencing shifts in the timing of sea ice breakup that can have severe implications on the amount and composition of organic matter food supply to the benthos. The role of benthic invertebrates in processing this sinking organic matter is typically classified by feeding types. The goal of this study was to evaluate if the classification of benthic invertebrates into feeding types is a useful concept for understanding the contribution of organic matter from various biosynthetic sources to benthic invertebrates across the Arctic Chukchi Sea. We used essential amino acid (EAA) specific stable isotope fingerprinting to identify proportional contributions of three EAA sources (bacterial, phytoplankton, terrestrial) as a proxy of carbon sources to the diets of suspension and deposit feeders and predators/scavengers. Across different feeding types, proportional contributions of EAA sources were similar, but showed significant differences among genera within the same feeding type, indicating that EAA use is genus-specific rather than feeding type-specific. These differences were attributed to other characteristics among genera, including mobility, selectivity of available EAA in sediments, and other trophic aspects such as assimilation efficiency. These characteristics provide useful additional considerations when grouping organisms by feeding types. High proportions of terrestrial EAA were found in the majority of benthic genera across feeding types and characteristics in this study, reflecting the high proportions of this matter source in sediments and confirming other recent findings that this source is being used by benthic consumers in the Arctic. EAA contributions to various benthic genera across the Chukchi Sea shelf had only weak correlations with environmental variables. With the distinctly different uses of different EAA sources by benthic-feeding genera, expected climate change-driven shifts in the supply of EAA sources to the Chukchi Sea shelf benthos may have implications for the composition of benthic communities and energy flow through the benthic food web, including energy pathways that support current top predators.

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2.2 Introduction

Benthic communities are an essential component of the marine ecosystem, playing a vital role in detrital decomposition and carbon and nutrient cycling of organic matter within the sediment (Hyland et al., 2005; Grebmeier, 2012; Wrede et al., 2017). Benthic fauna respond quickly to organic matter influx to the seafloor and readily use the incoming material, while their feeding and bioturbation activities influence the biogeochemical processes and fate of organic matter within the sediment (Kristensen and Holmer, 2001; Welsh, 2003; Witte et al., 2003; Mermillod-Blondin et al., 2005). The bioturbation activity of the benthos is dependent on the community abundance and composition, which in turn depend on food quantity and quality (Grebmeier and McRoy, 1989; Albertelli et al., 1999). Historically, fresh marine phytodetritus has been considered as the main high quality food source for benthic invertebrates; however, bacteria can modify this source and add nutritional value to organic matter (Heip et al., 1995; Lovvorn et al., 2005; McTigue and Dunton, 2017). Recent studies have shown that, although less nutritious than phytodetritus, terrigenous organic matter is being used by the benthos (Dunton et al., 2006; Kędra et al., 2012; Rowe et al., 2019). The use of terrigenous organic matter at the base of the food web can cause an increase in overall food web length, resulting in lower energy transfer efficiencies to higher trophic levels (Bell et al., 2016). This suggests that potential climate-related shifts in the composition of the organic matter supply to the benthos could result in a longer and less energy-efficient food-web (e.g., Dunton et al., 2006; Harris et al., 2018).

In regions of low productivity or highly seasonal production, the organic matter food supply can be a limiting resource for benthic communities, increasing competitive interactions (Levinton, 1972; Campanyà-Llovet et al., 2017). Benthic invertebrates can capture suspended organic matter from the overlying water-column, or gather is from the sediment-water interface, or from within the sediment (Walker and Bambach, 1974). Traditionally, the specific modes of food acquisition of benthic invertebrates, operationally characterized into broad feeding types (FT), can assist in reducing competition for the organic matter resource (e.g., Hunt, 1925; Word, 1979; Jumars and Gallagher, 1982; Włodarska-Kowalczuk et al., 2019). Among the main FTs of benthic shelf systems are suspension feeders (SF), surface deposit feeders (SDF), subsurface deposit feeders (SSDF), and predators/scavengers (P/S). Suspension feeders play an essential role in linking pelagic to benthic production by capturing relatively fresh, settling or resuspended particles out of the water column using cilia or mucus traps (Sokolova, 1972;

Walker and Bambach, 1974). Surface deposit feeders mostly forage on freshly deposited material on the sediment surface, while SSDF exploit material in deeper sediment horizons (Lopez and Levinton, 1987). Lastly, P/S are less directly coupled to the organic matter sources than other FTs and, instead, actively hunt their prey (P) or scavenge on dead organisms (S) (e.g., Walker and Bambach, 1974; Bluhm et al., 2009). The various feeding strategies of benthic invertebrates suggest that these FTs may rely on different organic matter sources to varying degrees, especially in a highly dynamic and seasonal system such as the Arctic shelf systems. If so, then the expected changes in the composition of organic matter supply due to climate warming in the Arctic are likely to have implications for benthic composition and ecosystem functioning (Węsławski et al., 2011; Kędra et al., 2015).

Over the last decades, the Arctic Ocean has been experiencing increasingly longer ice-free seasons and is predicted to be ice-free as early as 2040 (Overland and Wang, 2013; Laliberté et al., 2016). The reduction in sea ice allows increased heat fluxes, causing an earlier onset of sea ice retreat in spring and delaying ice formation in the fall, resulting in an overall longer ice-free period over the summer (Steele et al., 2008). Arctic shelf systems are especially vulnerable to these changes, as they experience warming three times the global average; specifically, the Chukchi Sea shows some of the fastest declines in sea ice cover across the Arctic (Steele et al., 2008; Serreze et al., 2009; Frey et al., 2015). Under cold climate regimes, almost 70 % of water primary column production escapes pelagic grazing and reaches the seafloor on the Chukchi Sea shelf, supporting a rich benthic community (Walsh et al., 1989; Lovvorn et al., 2003; Piepenburg, 2005; Grebmeier, 2012). Changes in the timing of sea ice breakup in a warming climate highly influence the strength and timing of pelagic and ice-associated production and can result in alterations in the food supply to the benthos (Grebmeier et al., 2006a). For example, the loss of sea ice reduces the strength of an early sea ice algal pulse to the seafloor, and climate-driven shifts in timing of open-water phytoplankton blooms could result in enhanced grazing pressure by zooplankton, causing lower quality and quantity of pelagic primary production to reach the benthos (Hunt et al., 2002; Lalande et al., 2007).

Pelagic production is considered the most important carbon source for Arctic benthic food webs (e.g., Iken et al., 2010; McTigue et al., 2015). External carbon subsidies, such as terrestrial organic matter, have traditionally not been viewed as a nutritious carbon source (Schell, 1983), but terrestrial organic matter has been acknowledged as an important source in benthic invertebrate food webs of other Arctic regions (e.g., Dunton et al., 2006; Iken et al., 2010; Divine et al., 2015; Bell et al., 2016; Rowe et al., 2019). Multiple carbon sources can greatly contribute to the overall stability of Arctic food webs and energy flow

through the system (McMeans et al., 2013). Terrestrial organic matter already contributes ~15 % of sediment carbon budget in the Chukchi Sea but can contribute over half the total sedimentary carbon in some Chukchi Sea regions (Morris et al., 2015; Chapter 1). Seasonal input of terrigenous carbon in the Arctic is controlled by river discharge, coastal erosion, and glacial melt and has increased since the 1970s (McClelland et al., 2006). Across the Arctic, river discharge has increased on average by ~120 km^3 y^{-1}, which could allow for higher proportions of this material to be available to the shelf benthos (Macdonald et al., 1998; Guo et al., 2004; Goñi et al., 2005; Yunker et al., 2005; McClelland et al., 2006). As an additional biosynthetic organic matter source, sediment bacteria associated with detrital particles can add greatly to the nutritional value of sedimentary organic matter (e.g., Newell, 1965; Heip et al., 1995). An increase in bacterial production and biomass within sediments with increases in bottom water temperatures on Arctic shelves, may increase the importance of bacteria as a food source to benthic consumers (Kirchman et al., 2009; Kritzberg et al., 2010; Wang et al., 2012).

The importance of various primary production sources to Arctic benthic communities has received increased attention in recent years but information on if and how benthic FT differently use organic matter from various primary producers is still scant. If they do, climate change-induced alterations to the relative proportions of marine photosynthetic (phytoplankton and ice algae), terrestrial, and bacterial production of Arctic shelf systems could result in a rearrangement of benthic FT structure and subsequent changes to benthic energy flow, as has been suggested for Antarctic benthic systems (e.g., Lohrer et al., 2012; Dayton et al., 2019). Here, we used essential amino acid specific stable isotope fingerprinting to determine the relative proportional contributions of various biosynthetic sources (bacterial, phytoplankton, terrestrial) to benthic invertebrate diets. The approach is based on the observation that broad phylogenetic classes of biosynthetic sources display characteristic patterns (fingerprints) of essential amino acid (EAA) carbon isotope ratios (Larsen et al., 2009; Larsen et al., 2013; Larsen et al., 2015). As EAA, their isotope ratios are then conserved in consumer tissues and can be used to determine the proportional contribution of sources to consumers (Larsen et al., 2009). This approach is more specific than the often-used bulk stable isotope analysis, as it refers to a fraction of the total organic matter and allows higher specificity to determine biosynthetic sources. Here, this method was used to distinguish between organic matter derived from bacterial, marine phytoplankton, and terrestrial production as sources that may experience proportional changes with warming Arctic shelves. The aim of this study was to determine the proportional contributions of these three biosynthetic EAA sources to four major benthic invertebrate FT across the Arctic Chukchi Sea shelf. We hypothesize that relative proportional

contributions of these EAA sources will vary depending on FT, and that the FT concept provides a useful ecological approach to address resource and trophic niche use.

2.3 Materials and Methods

2.3.1 Sample collection

During the Arctic Marine Biodiversity Observing Network (AMBON, www.ambon-us.org) cruise in August 2015, tissue samples of benthic invertebrates were collected for amino acid carbon stable isotope analysis to determine proportional contribution of various EAA sources (bacterial, phytoplankton, terrestrial) to benthic FTs. Invertebrates were collected using a plumb-staff beam trawl and van Veen grab at 15 station across the Chukchi Sea shelf between 30 and 54 m water depth (Fig. 2.1). Ten common benthic invertebrates representing four major FTs were collected (Table 2.1). Invertebrates were treated here at the genus level, except for the family Maldanidae. The gastropod genus *Buccinum* contained individuals of the species *B. polare* and *B. scalariforme,* and the bivalve genus *Macoma* comprised individuals of the species *M. calcarea* and *M. moesta*. Other genera were represented by the following species: *Chionoecetes opilio*, *Eualus gaimardii gaimardii*, *Nuculana radiata*, *Serripes groenlandica*, *Alcyonidium gelatinosum*. The amphipod *Anonyx* sp. and the shrimp *Argis* sp. were only identified to genus level. Echinoderm species (*Leptasterias groenlandica*, *Leptasterias polaris*, *Ophiura sarsii*, *Myriotrochus rinkii*) were initially included in the analysis; however, they were eliminated because not enough amino acids could be extracted for analysis. One individual per genus was collected per station, where available, and individuals from different stations were used as replicates for analyses (see below). Not all taxa occurred at all stations, but representatives of all FTs occurred at each of the stations. To reduce variability in isotope values due to ontogenetic stage and metabolic turnover time of specific tissues (Gannes et al., 1997; Jardine et al., 2006; Blanchet-Aurigny et al., 2012; deVries et al., 2015; Lefebvre and Dubois, 2016), the same stages (adult) and tissue types were collected for the same taxa (Table 2.1). All tissues were dried for 24 h at 60°C to constant weight and transported back to the University of Alaska Fairbanks (UAF) laboratory for further processing and analysis.

2.3.2 Essential amino acid stable isotope fingerprinting

For EAA extraction, dried invertebrate tissue samples were individually weighed (2 – 5 mg) and transferred into culture tubes, 1 mL 6 N HCl added, sealed, and flushed with N_2 to prevent oxidation, and hydrolyzed at 110°C on a heating block for 20 h (following methods described by Larsen et al., 2013). Samples were lipid-extracted by adding 2 mL n-hexane:dichloromethane (DCM) (6:5, v:v) and vortexed

for 1 min to remove lipophilic compounds. The bottom aqueous phase containing amino acids (AA) was retained and transferred into a 3 mL BD™ syringe connected to a 0.2 µm Millex-GP™ filter to remove any excess tissue material. Then, 0.25 µl of 0.1 N HCl was added into the syringe to rinse the filter and remove remaining AA. An internal standard, norleucine (Sigma-Aldrich, BCBQ0497V) (25 µl) was added to each sample, and the sample was evaporated to dryness under constant N_2 flow in a 60°C water bath. Dried samples were converted into volatile AA isopropyl esters by adding 2 mL of acidified 2-propanol to each sample; the sample was then caped and heated to 110°C on a heating block for 60 min. After cooling, samples were evaporated to dryness under constant N_2 flow at 60°C. Samples were washed twice with 0.5 mL DCM and evaporated to dryness at room temperature under a constant stream of N_2. To each sample, 0.5 mL trifluoroacetic acid (N-TFA) and 0.5 mL DCM were added to acetylate samples, heated at 100°C for 10 min, cooled, and evaporated to dryness at room temperature under a constant stream of N_2. Samples were then rinsed with DCM as described above. Ethyl acetate (250 µl) was added to each sample, and samples stored at -20°C until further analysis.

All AA extracts were analyzed in triplicate and five EAA isolated: isoleucine (Ile), leucine (Leu), phenylalanine (Phe), threonine (Thr), valine (Val). Additionally, to account for analytical variability among different extraction batches, a homogenized sample of the Arctic caridean shrimp *Sabinea septemcarinata* was extracted and analyzed for carbon isotope ratios with every run to assess analytical variability. Carbon isotope ratios values were determined by gas chromatography combustion isotope ratio mass spectrometer (GC-C-IRMS) using a Thermo GC-IsoLink II sytem (ThermoFisher Scientific) coupled to a Delta V IRMS via the Conflo IV gas interface. The Thermo Trace GC was equipped with an HP ULTRA-1 column (Agilent, 50 m x 0.32 mm x 0.52 µm) at the UAF Alaska Stable Isotope Facility (ASIF). The following temperature program was used: 60°C (3 min), 110°C (3°C min^{-1}) for 5 min, 190 °C (3°C min^{-1}) for 5 min, and increasing at a rate of 10°C min^{-1} to 280°C (8 min). Samples were injected using a split/splitless inlet (280°C): injection volume 0.3 µL, carrier flow 0.8 min^{-1}, split flow 50 mL min^{-1}, purge flow 5.0 min^{-1}, split flow 50 mL min^{-1}, splitless time 1.0 min.

Stable isotope ratios are reported in delta (δ) notation as $((R_{sample}/ R_{standard}) -1) \times 1000‰$, where R is the ratio of heavy to light isotope, and the standard for carbon was Vienna Pee Dee Belemnite (VPDB). Correction factors for each EAA were calculated from known reference values for $\delta^{13}C$ values of pure EAA according to O'Brien et al. (2002) to account for carbon addition and fractionation during the EAA derivatization process. Each EAA $\delta^{13}C$ value was normalized relative to the mean $\delta^{13}C$ value across all EAA for that sample ($\delta^{13}C_{EAA\_normalized} = \delta^{13}C_{EAA\_measured'} - \text{mean } \delta^{13}C_{EAA'}$) (Rowe et al., 2019). The normalized EAA $\delta^{13}C$ values were distinct among biosynthetic sources included in this study: bacteria, diatoms

(representative of dominant Arctic phytoplankton), and terrestrial plants, and were used as endmembers in a stable isotope mixing model.

2.3.3 Statistical analysis

Reference $\delta^{13}C_{EAA}$ values for bacteria were obtained from Larsen et al. (2013) and for diatoms and terrestrial plants from Rowe et al. (2019). $\delta^{13}C_{EAA}$ values of endmembers and of tissue samples were used in a stable isotope mixing model in R: (SIMMR, https://cran.r-project.org/web/packages/simmr/vignettes/simmr.htmL) to determine proportinal contributions of EAA from these endmembers to invertebrate tissues. EAA sources in tissue samples were considered a proxy for carbon contribution to invertebrate diets.

Statistical analyses were performed in R using the RStudio (http://www.rstudio.com) interface version 1.1.383 and in Primer-e version 7.0.13 for multivariate analyses. Prior to parametric statistical analyses, normality was tested using a Shapiro-Wilks test, homogeneity of variance using Levene's test, and independence using a chi-squared test. If necessary, data were square root transformed, to meet assumptions, except when analyzing for significant differences among organic matter source contributions within FTs, SF data were cube root transformed. Significant differences in proportional contributions of each EAA source among FTs (genera within FT considered as replicates) were determined using one-way analysis of variance (ANOVA) with Tukey's honest significant difference post-hoc test at a significance level of $\alpha = 0.05$. Differences in EAA contributions from bacterial, phytoplankton, and terrestrial sources were also assessed among genera within each FT (ANOVA, using individuals from the various sampling stations within each genus as replicates). A PERMANOVA was conducted to determine significant differences of proportional contributions of the three carbon sources to all genera.

A BEST analysis was used to determine potential relationships between average proportional contributions of all endmembers to each FT and environmental variables (PRIMER-e version 7.0.13). Environmental data were collected by collaborators during the research cruise (available on the Marine Biodiversity Observing Network (MBON) data portal, https://mbon.ioos.us/; data access: https://doi.org/10.25921/zqwr-at45) and included bottom temperature, bottom salinity, sediment grain size, sediment chlorophyll-*a* content, sediment total organic carbon, sediment C/N ratios, and bulk sediment stable carbon and nitrogen isotope compositions (presented as $\delta^{13}C$ and $\delta^{15}N$ values) (Table 2.2).

2.4 Results

Proportional EAA contributions of bacterial, phytoplankton, and terrestrial organic matter sources to the four FTs were highly variable, and did not differ systematically among FT (ANOVA $p>0.05$; Fig. 2.2). To investigate whether these contributions were different within each FT, we found slightly elevated proportions of terrestrial EAA in SF and SDF, and higher bacterial EAA in SSDF and P/S relative to other endmembers, but these endmember EAA contributions were not significantly different within each FT (ANOVA $p>0.05$; Fig. 2.3).

To investigate if part of the high variability in EAA contributions within each FT could stem from the various genera contributing to each FT, we analyzed EAA contributions for each genus separately. Proportional EAA contributions were highly variable with some significant differences among the genera within the same FT (Fig. 2.4). For example, the SF bryozoan *Alcyonidium* had a significantly higher terrestrial EAA contribution compared with the other SF genus, *Serripes* (PERMANOVA; $p = 0.015$). As *Macoma* was the only genus analyzed within SDF, no source EAA differences could be determined for this FT. The SSDF Maldanidae and *Nuculana* showed slight (e.g., higher bacterial EAA in Maldanidae) but non-significant differences in EAA contributions. *Buccinum* had significantly higher proportions of terrestrial organic matter EAA compared to all other P/S genera (PERMANOVA; $p < 0.05$ in all comparisons).

Given the differences in EAA source contributions observed among different genera within the same FT, we visually assessed how consistent EAA source contributions were for individual species within each genus, and if there were any obvious spatial trends across the sampling region within each genus. Patterns in EAA contributions were relatively consistent for individuals at most sampling stations across the Chukchi sea shelf for *Macoma*, *Eualus*, *Argis*, *Chionoecetes*, and *Buccinum*, although some stations were distinctly different in EAA source proportions (Fig. 2.5). Different stations were distinct in their EAA contributions to the various genera so that no consistent spatial trend explaining the variability could be discerned. For *Buccinum* and *Macoma*, these station differences did not correlate with the specific species within these genera analyzed at these stations. Other genera such as *Nuculana* and *Serripes* had highly variable EAA source contributions across the shelf, but the low level of station replication for those taxa did not allow discerning any spatial trends. Correlations between EAA source contributions and most environmental variables were low to moderate for most genera ($\rho < 0.5$, BEST analysis); however, *Macoma* ($\rho = 0.73$) and *Nuculana* ($\rho = 0.77$) EAA patterns had high, positive correlations with sediment $\delta^{13}C$ and sediment chl-*a* concentration, respectively.

3.5 Discussion

The benthos plays a vital role for ecosystem processes including detrital decomposition, nutrient cycling, and energy flow to higher trophic levels (Hyland et al., 2005). Environmental conditions strongly influence the presence and success of benthic faunal assemblages and the supply of OM sources to the benthos, especially in the Arctic Ocean (Grebmeier et al., 2015). These conditions are prone to changes with ongoing climate change and have the potential to alter the composition of food sources available to benthic organisms (Dunton et al., 2006; McMahon et al., 2006; Søreide et al., 2006). Equally, the composition of benthic FT can provide insights if and how these food resources are being used. The goal of this study was to identify how three EAA sources (bacterial, phytoplankton, terrestrial) contribute to the diet of four major benthic invertebrate FTs across the Chukchi Sea shelf. While there were trends of elevated contributions of terrestrial EAA to SF and SDF and of bacterial EAA to SSDF and P/S, results were highly variable, and differences among FT were not significant. High variability within FTs originated from differences in EAA contributions to the various genera assigned to each FT. These results indicate that the conventional FT classification alone is not sufficient to effectively characterize OM use by benthic invertebrates on the Chukchi Sea shelf, and that additional genus-level attributes may need to be considered to adequately categorize benthic feeders.

Many benthic invertebrates consume settling or resuspended material near the sediment surface as well as OM within the sediment itself, making OM the main food source for these organisms (Carey, 1991; Feder et al., 2010; Kędra et al., 2012). Invertebrates are typically assigned to general FTs, classifying their use of the sedimentary OM sources mostly according to the morphology of their mouth parts and body positioning above, on, or within the sediment (Graeve et al., 1997). Contrary to expectation, we did not find significantly different proportional contributions of three major EAA sources (bacterial, phytoplankton, terrestrial) based on FT. This could be due to the fact that Chukchi Sea sediments do not show strong patterns in relative distribution of these same EAA sources across the top 5 cm of sediment (Chapter 1), a result of the high bioturbation activity of the rich Arctic benthic communities. Therefore, although the four FTs distinguished in this study live and feed in different sediment layers, the lack of depth-related trends in EAA source distribution within the sediment likely resulted in overall similar trends among FTs. This supports previous studies that found Arctic benthic SDF and SSDF to be isotopically indistinguishable when analyzing bulk tissues, even though they are feeding on different sediment horizons (Dunton et al., 2014; North et al., 2014; McTigue and Dunton, 2017). Different from the particle-based FTs, the diet of P/S is typically comprised of a variety of prey items that themselves are of different

feeding modes and diet specialization. This can lead to an integration and homogenization of isotopic signatures of endmember biomarker EAA in the P/S (McTigue and Dunton, 2017).

The lack of significant differences among FTs in proportional contributions of endmember EAA was attributable to the high variability among the genera assigned to the same FT. Besides their general FT classification, these genera have specific, additional characteristics that can account for different use of food resources within the same FT (e.g., Bonsdorff and Pearson, 1999; Bremner et al., 2006). Such characteristics can include mobility, feeding selectivity, and assimilation efficiency. For example, mobility of a given taxon can strongly influence the resource availability that can be exploited by that taxon (Ojeda and Dearborn, 1991). Mobile organisms are able to actively search or use chemical cues to detect high quality food areas, while sessile organisms are limited to the local availability of carbon sources (Iken et al., 2001; McTigue and Dunton, 2017). This is particularly evident in P/S, which are usually more mobile than other FT and consume a wide variety of prey items (McCann et al., 2005; Nordström et al., 2009; Kędra et al., 2012). Some mobile P/S are omnivorous and use a broad diet, ranging from some detrital matter to invertebrate prey to fish carrion; a representative example in our study is the snow crab, *Chionoecetes* (Divine et al., 2015). The decapod P/S *Eualus* spp. exhibits even higher mobility and regularly extends its foraging forays into the water column and even onto sea ice in the Arctic (Birkely and Gulliksen, 2003; Nygård et al., 2007), a strategy known to diversify diet and the overall food web (Iken et al., 2001). Less mobile P/S, such as the gastropod *Buccinum*, are categorized as opportunistic generalists that use a smaller range of prey items. The reduced mobility in a taxon like *Buccinum* limits its ability to exploit a wide variety of prey items, and gut content analysis showed that this genus uses high amounts of OM (Bearhop et al., 2004; Smith and Thatje, 2013; Montgomery et al., 2017). The use of direct OM sources, likely due to lowered mobility, could account for the higher proportion of terrestrial EAA in *Buccinum* compared with other P/S, as terrestrial EAA were abundant in Chukchi sediments (Chapter 1). Hence, the proportional EAA contributions in many P/S seem less derived from direct consumption of detrital matter but reflect the EAA sources consumed by their prey organisms, which can be highly diverse in the more mobile P/S (Wieczorek and Hooper, 1995; Lovvorn et al., 2005; Divine et al., 2015).

In contrast to highly mobile taxa, sessile or discretely mobile organisms are restricted to the food sources available at their specific location and have reduced ability to search for areas of fresh, highly nutritious food (North et al., 2014; McTigue and Dunton, 2017). Most sessile to discretely mobile SF and DF are restricted to the use of locally available food. The SDF bivalve *Macoma* is an example of a mostly sessile feeder, living buried within the sediment and sweeping the surrounding surface OM deposits with

its siphon (Reid and Reid, 1968; Macdonald et al., 2010). It stands to reason that *Macoma* depends on the locally available OM sources. *Macoma* in the Bering Sea and northern Chukchi Sea consumes mostly microalgal sources, based on compound-specific stable isotope analyses (Oxtoby et al., 2016; Rowe et al., 2019), but also uses older organic material from deeper sediment layers (North et al., 2014). Consistent with the latter, we detected larger contributions of terrestrial EAA than phytoplankton EAA in this genus, which reflects local endmember availability in the sediments. Similarly, the sessile SF bryozoan *Alcyonidium* is limited to food source availability at the particular locations where it occurs (Macdonald et al., 2010). As a SF, we would have expected this genus to rely mostly on microalgae (Riisgård and Patricio, 1997) but instead, *Alcyonidium* also contained a high proportion of terrestrial EAA. This likely reflects *Alcyonidium*'s overall high adaptive ability to local environments (Kuklinski and Porter, 2004), resulting in its opportunistic use of multiple organic matter sources that are available in the sediment. Another SF is the Greenland cockle, *Serripes*, which is situated within the surface sediment and filters settling and resuspended particles from the water column (Ambrose et al., 2006; Kilada et al., 2007). However, like other cockles, it can become highly mobile through leaping movements with their strong foot when exposed from the sediment (Ansell, 1969; Richardson et al., 1993; Barnes, 1998). This could explain the lesser contribution of terrestrial EAA in *Serripes,* as they could seek different feeding patches if their preferred phytoplankton food is locally depleted. However, low mobility and the associated restriction to only consume available organic matter sources in surrounding sediments cannot be the only explanation of the differences in EAA contributions to various genera we observed in this study. Other low-mobility taxa, such as the bivalve *Nuculana* and the polychaetes Maldanidae should have similar proportions of EAA sources as *Macoma* and *Alcyonidium*, which was not the case.

The ability of organisms to select for a certain quality or size of food particles could influence the proportional contributions of EAA sources within different FTs and genera, in addition to mobility (Sainte-Marie, 1986). Particle selectivity is most common within DF and SF. For example, while many DF unselectively consume bulk sediments, others have behavioral or morphological adaptations to select high quality food particles (Hansen and Josefson, 2004). The SDF *Macoma* in our study consumed high proportions of terrestrial EAA, while it prefers freshly deposited phytoplankton or ice algal material in other Arctic regions (McMahon et al., 2006; Sun et al., 2007; Sun et al., 2009). We attribute part of our results to the low mobility in this taxon, but *Macoma* can also be a highly selective feeder, choosing particles for ingestion within the mantle cavity and ejecting remaining material in form of pseudofeces (Self and Jumars, 1988; Webb, 1993). Particle selection in *Macoma* is primarily for smaller particles like flagellates, bacteria, and microalgae that are smaller than 20 µm; even large diatoms can be rejected and

discarded (Reid and Reid, 1968; Hylleberg and Gallucci, 1975; Webb, 1993). While our results for *Macoma* do not allow us to draw any conclusions on particle size selection, it is possible that they selected for smaller terrestrial organic matter particles from the overall particle size range available in the sediment. Suspension feeding is another FT that often selects for particle quality and size to optimize food intake and energy gain (Reiswig, 1971; Willows, 1992; Orejas et al., 2003). Our finding of a high proportional contribution of phytoplankton (~50 %) to the diet of the SF cockle *Serripes* supported the notion of at least some selective feeding on microalgae, a common target for SF (Rosa et al., 2017). *Serripes* can be a selective feeder on microalgae (Ambrose et al., 2006), limited in particle size uptake by the size of the food groves on the gills. This also mirrors previous findings for this genus based on bulk stable isotope analysis that indicated tight links to marine-derived primary production and a low trophic level in various regions of the Arctic (Iken et al., 2010; Kędra et al., 2012). The SF bryozoan *Alcyonidium* is known to be highly size selective, often for small microalgae, using ciliary filter feeding to strain particles out of the water and transport them to the mouth opening (Nielsen, 2002). The high (~65 %) proportion of terrestrial EAA we found in this genus is different from previous investigations that determined *Alcyonidium* as exclusive phytoplankton-derived matter consumers in the Arctic Basin (MacDonald et al., 2010). However, in the Arctic coastal Beaufort Sea, *Alcyonidium* was estimated to contain about 20 % terrestrial contributions in its diet based on bulk stable isotope analysis with mostly omnivorous feeding habits (Harris et al., 2018). If *Alcyonidium* is selecting for small particle sizes, they may be choosing small particles from the terrestrial organic matter in our study area. These results support the suggestion that many SF in the Arctic tend to be more selective (Kędra et al., 2012).

Aside from selectivity for particle sizes, the efficiency at which organisms are able to assimilate certain types of food sources can vary among species. Microalgae are generally considered a high-quality marine food source selected by some organisms to gain maximum nutritional value (McMahon et al., 2006). However, the silicate frustrule of diatoms can make them resistant to digestion, and especially organisms with low digestive efficiency are not able to fully assimilate this source (Barillé and Cognie, 2000; Thomas and Blair, 2002; Hansen and Josefson, 2004). For the SSDF *Nuculana* and maldanid worms, experimental studies have shown low digestive efficiency of diatomaceous material and significant fractions of diatoms survived the digestive processes (Thomas and Blair, 2002; Hansen and Josefson, 2004). These findings could explain our results of relatively low contributions of phytoplankton EAA to the SSDF diets. *Nuculana* is buried in the sediment just below the sediment surface, and as a discretely mobile and non-selective feeder, it consumes food sources available within the surrounding sediment (Yonge, 1939; Lopez and Cheng, 1982). *Nuculana* also has high absorption efficiencies of sediment-associated

bacteria (Cheng and Lopez, 1991; Stead et al., 2003; Hansen and Josefson, 2004), probably explaining our finding of ~40 % bacterial EAA in this genus. To the best of our knowledge, assimilation efficiencies are not known for Maldanidae, but these low mobility, head-down feeders can have high ingestion rates of smaller particle sizes (Kudenov, 1982); this could indicate relatively high ingestion, and possibly assimilation, of bacterial material as we found in our study.

Relative contributions of EAA sources were fairly consistent for most genera across the sampling region, although contributions were drastically different at some stations for those genera where sufficient coverage enabled us to discern trends. Our previous research has shown that EAA proportions of bacteria, phytoplankton, and terrestrial organic matter in Chukchi Sea sediments were not different across the same sampling stations, and relations of sediment EAA to hydrographic conditions were low (Chapter 1). Similarly, we found here that correlations of EAA proportions in the various genera with environmental variables were typically low, except for select taxa, and some variables that are good indicators of food quantity and quality (sediment chl-*a* for *Nuculana* and $\delta^{13}C$ values for *Macoma*). High sediment chl-*a* values usually represent high settlement rates of pelagic production, and $\delta^{13}C$ values around -22 ‰ are indicative of phytoplankton material (Naidu et al., 2000; Grebmeier et al., 2006b; McTigue et al., 2015). Neither bivalve taxa had particularly high proportional contributions of phytoplankton EEA to their diet, but closer inspection of the data showed that there were some strong relationships between the diet phytoplankton EEA and these sediment variables in some individuals and locations, which likely drove these high correlations. It is important to note that we present EAA sources in invertebrates as proportional contributions and not absolute quantitative measurements. Hence, the correlations to environmental variables, which are based on absolute values, may be spurious and need to be considered with care.

The fact that correlations with most environmental variables were weak could also be related to a mismatch in sampling scale of those variables and the invertebrate taxa. In particular, sediment parameters were collected from van Veen grabs that represent a small area of the seafloor, while invertebrates were collected from trawls that swept several hundred square meters in the station vicinity (Iken et al., 2019). Because sediment characteristics can vary over small spatial scales of centimeters to meters (Watling, 1988; Danovaro et al., 2001), it is possible that the sediment parameters did not accurately reflect the specific conditions at the location of animal collection, especially for sessile or discretely mobile taxa. In addition to a possible spatial mismatch, a temporal offset could also play a role. Sediment conditions, such as OM quantity and quality, change rapidly over temporal scales (Danovaro et

al., 2001; Dell'Anno et al., 2003), while the EAA contributions determined for the consumers are the result of slow turnover rates in Arctic invertebrates, likely on the order of months, based on bulk stable isotope experiments (Kaufman et al., 2008; Weems et al., 2012).

In conclusion, results from this study showed that proportional contributions of three major EAA sources (bacterial, phytoplankton, terrestrial) were more genus-specific than FT-specific in benthic invertebrates on the Chukchi Sea shelf. Based on our research, we suggest that when grouping organisms into broader categories, such as FT, additional characteristics should be considered. Specifically, mobility of organisms that allows them to seek out food patches, selectivity in particle intake, and possibly differences in assimilation of specific food sources could account for some of the differences of genera within FT. Categorizing taxa by FT is still a useful approach, but with the understanding that additional characteristics add variability within a FT. These findings are in agreement with the increasing use of functional traits analyses, where multiple characteristics are used to describe and categorize species trophically (e.g., Bremner et al., 2006). Although terrestrial organic matter has traditionally been considered a negligible food source for benthic invertebrates (Schell, 1983), this source made up a large EEA fraction (>25 %) in seven out of ten invertebrate genera. This supports other recent Arctic studies that have also found high amounts of terrestrial and bacterial matter in benthic invertebrate diets using a variety of biomarker approaches (e.g., Dunton et al., 2006; Bell et al., 2016; Harris et al., 2018; Rowe et al., 2019). Current trends in climate warming increase coastal erosion and river discharge, the two main vectors of terrestrial matter delivery to the Arctic shelf (Yunker et al., 2005; Bopp et al., 2001; McClelland et al., 2006; Lantuit et al., 2012). This, and other climate-related shifts in primary production levels, such as increased phytoplankton production under ice-free conditions (Brown and Arrigo, 2013) or higher bacterial production in warmer waters (Pomeroy and Deibel, 1986; Kirchman et al., 2009), can have major impacts on future benthic invertebrate diets. Because the supply and quality of food are major drivers for benthic community composition on polar shelves (Grebmeier et al., 2015; Jansen et al., 2018), shifts in OM supply can change the composition of benthic FT with possible implications for higher trophic levels, such as marine mammals using the benthos as feeding ground (Oxtoby et al., 2017; Moore and Huntington, 2008).

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2.7 Figures and tables

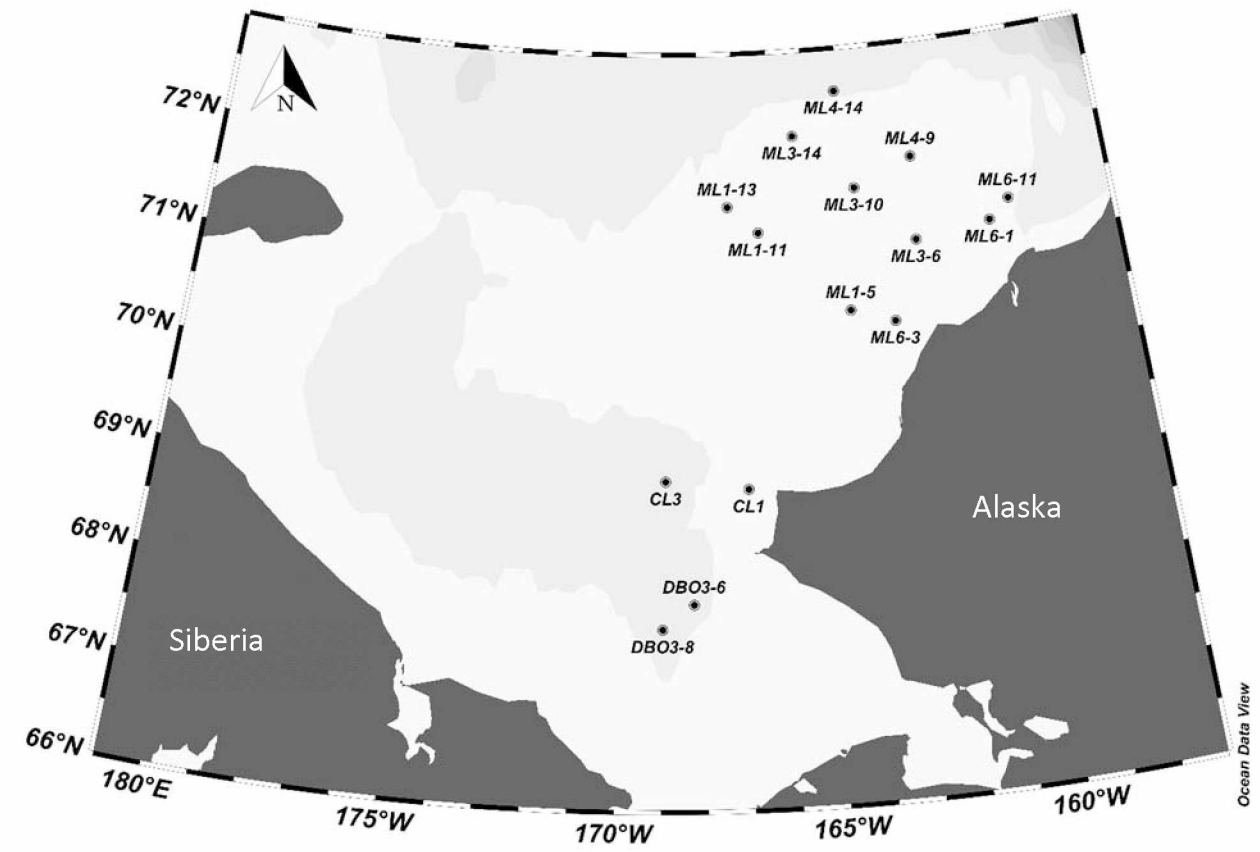

Figure 2.1: Chukchi Sea shelf stations (black dots labeled with station ID) sampled for benthic invertebrates during the AMBON 2015 cruise. Dark shades indicate the 50 m isobath on the shelf.

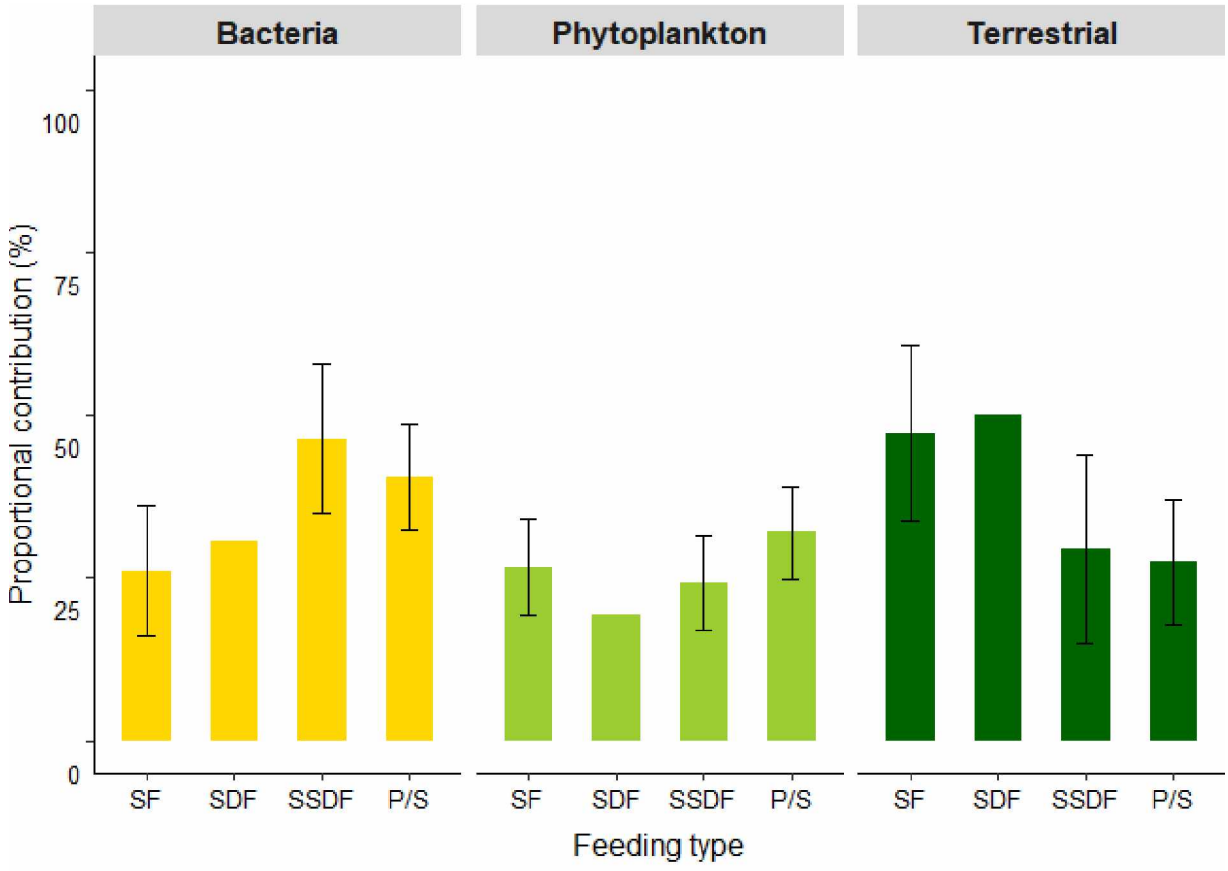

Figure 2.2: Mean proportional contributions (%, mean ± 1 SD) of three essential amino acid sources (bacterial, phytoplankton, terrestrial) for each benthic invertebrate feeding type (SF n=2, SDF n=1, SSDF n=2, P/S n=5) across the Chukchi Sea shelf. Feeding type classifications are: SF – suspension feeders, SDF – surface deposit feeders, SSDF – subsurface deposit feeders, P/S – predators/scavengers. Proportional essential amino acid contributions were not significantly different among feeding types.

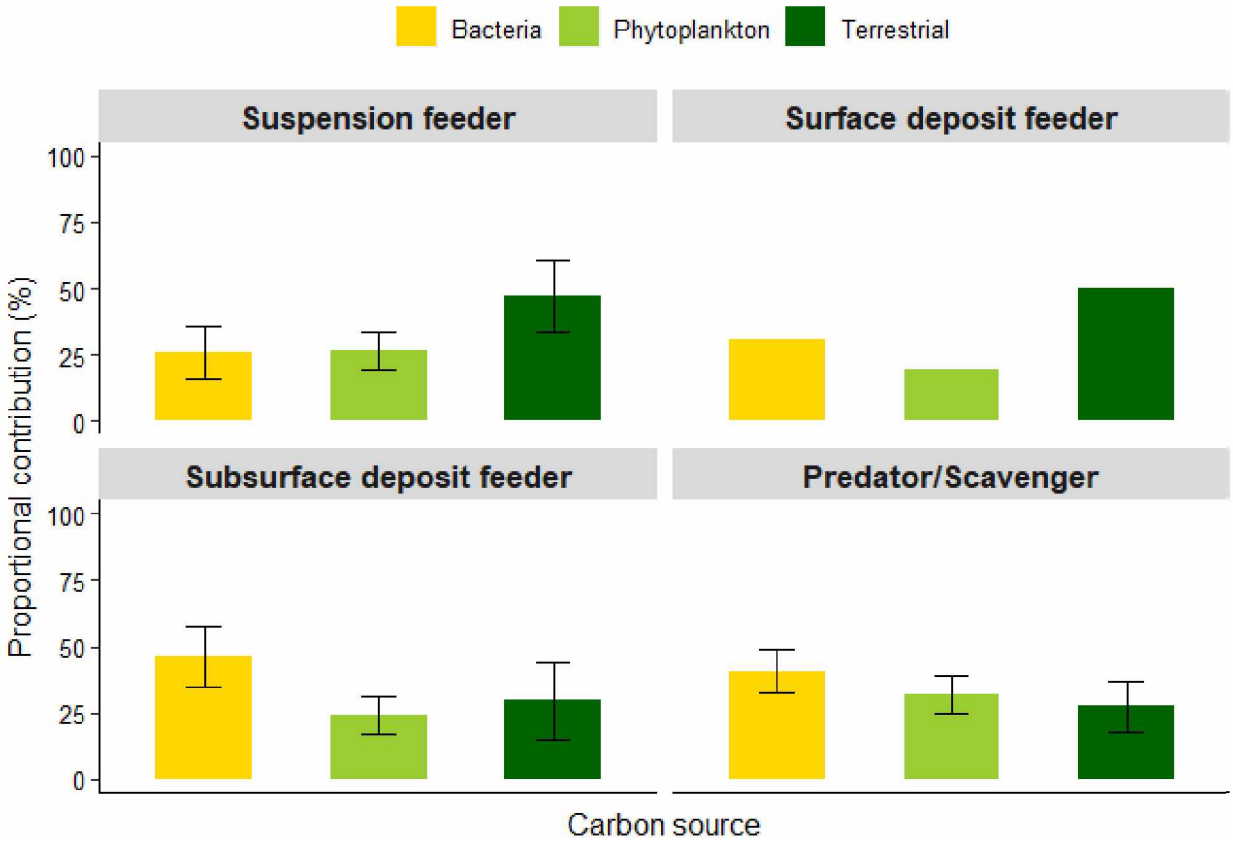

Figure 2.3: Mean proportional contributions (%, mean ± 1 SD) of three essential amino acid sources (bacterial, phytoplankton, terrestrial) within each benthic invertebrate feeding type (SF n=2, SDF n=1, SSDF n=2, P/S n=5) across the Chukchi Sea shelf. Feeding type classifications are: SF – suspension feeders, SDF – surface deposit feeders, SSDF – subsurface deposit feeders, P/S – predators/scavengers. Proportional essential amino acid contributions were not significantly different within each feeding type.

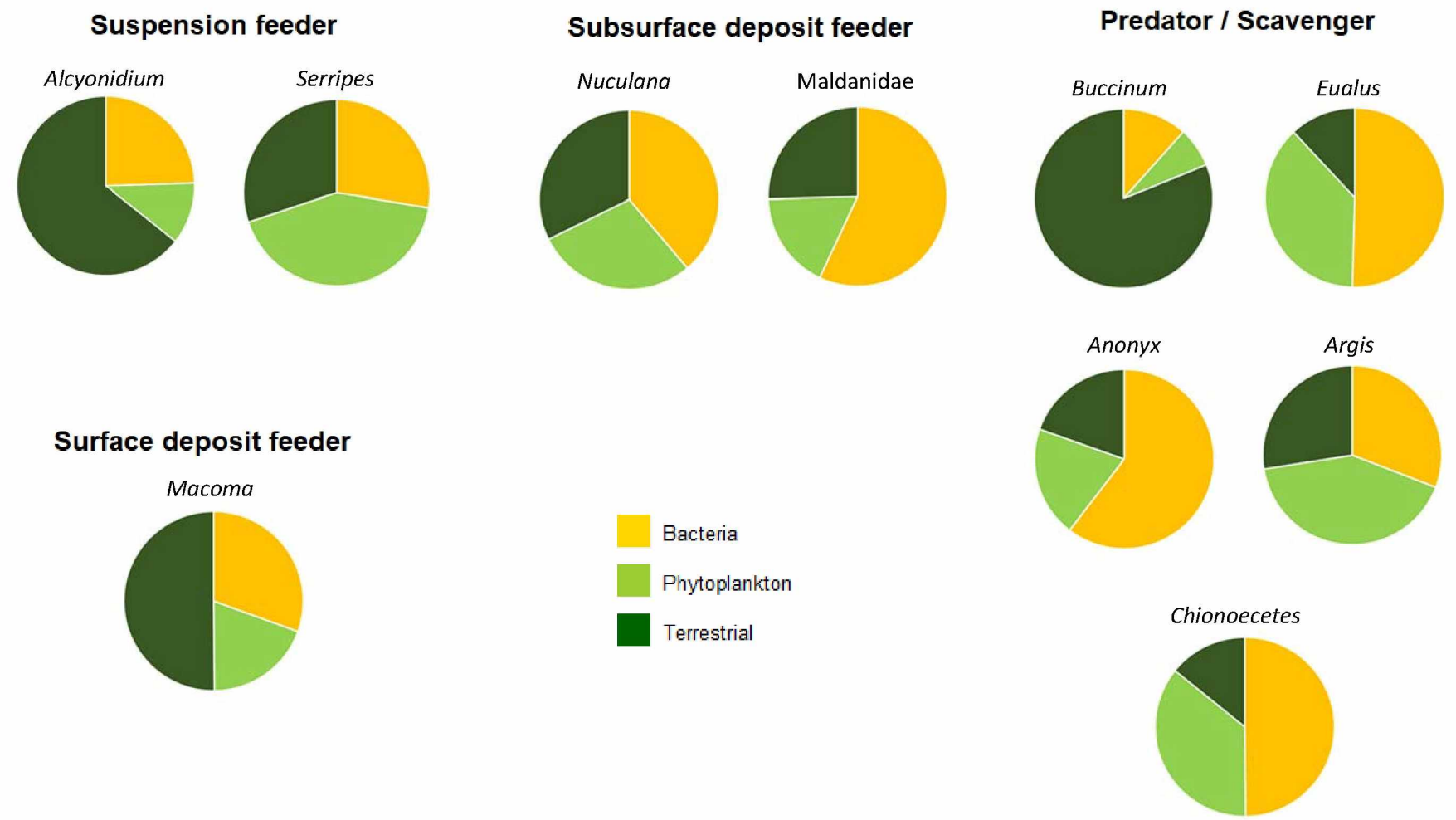

Figure 2.4: Mean proportional contributions (%) of three essential amino acid sources (bacterial, phytoplankton, terrestrial) within each benthic invertebrate genus belonging to four major feeding types across the Chukchi Sea shelf. Feeding type classifications are: SF – suspension feeders, SDF – surface deposit feeders, SSDF – subsurface deposit feeders, P/S – predators/scavengers.

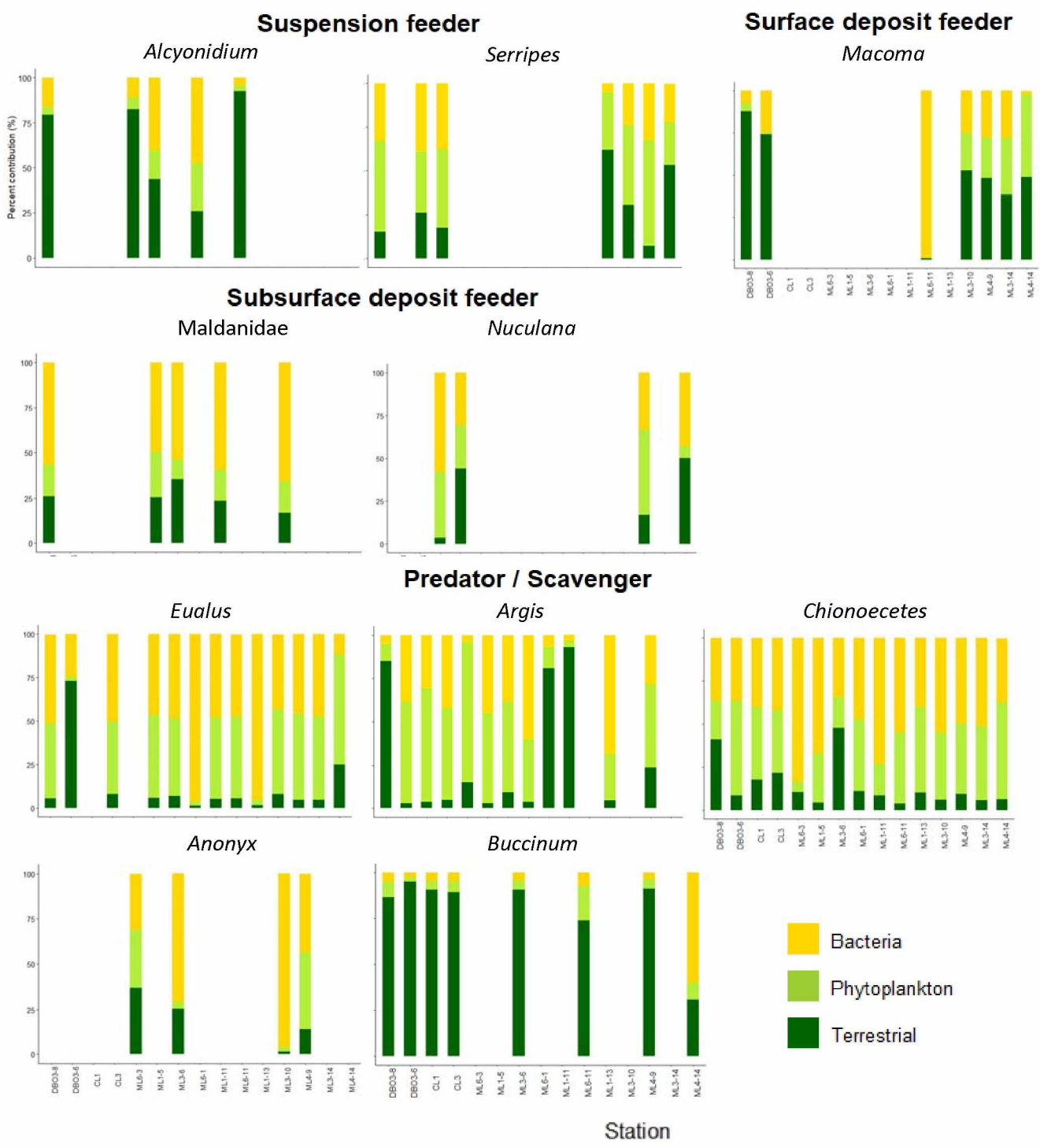

Figure 2.5: Proportional contributions (%) of three essential amino acid sources (bacterial, phytoplankton, terrestrial) for each benthic invertebrate genus within each feeding type across sample stations (n=1 individual per station) across the Chukchi Sea shelf. Stations are ordered from southern to northern Chukchi Sea based on latitude (see map in Fig.

2.1). Feeding type classifications are: SF – suspension feeders, SDF – surface deposit feeders, SSDF – subsurface deposit feeders, P/S – predators/scavengers.

Table 2.1: List of genera included in this study, their representative feeding type, tissue type, and total number of individuals sampled (n), with one individual per station. Feeding type classifications are: SF – suspension feeders, SDF – surface deposit feeders, SSDF – subsurface deposit feeders, P/S – predators/scavengers.

Taxon	**Species**	**FT**	**Tissue**	**n**
Bivalvia	*Serripes groenlandica*	SF	muscle	7
Bryozoa	*Alcyonidium gelatinosum*	SF	whole	7
Bivalvia	*Macoma* spp.	SDF	muscle	7
Bivalvia	*Nuculana radiata*	SSDF	muscle	7
Polychaeta	*Maldanidae*	SSDF	Body wall	5
Amphipoda	*Anonyx* sp.	P/S	whole w/o gut	12
Decapoda	*Argis* sp.	P/S	muscle	15
Decapoda	*Chionoecetes opilio*	P/S	muscle	13
Decapoda	*Eualus gaimardii gaimardii*	P/S	muscle	8
Gastropoda	*Buccinum* spp.	P/S	muscle	4

Table 2.2: List of environmental variables at all sample stations on the Chukchi Sea shelf during AMBON 2015 cruise including depth (m), bottom water temperature (°C), bottom water salinity, sediment grain size (% phi), surface sediment chlorophyll-*a* content (mg/m^2), surface sediment $\delta^{13}C$ (‰), $\delta^{15}N$ (‰), total organic carbon (%), and carbon to nitrogen (mass of C:mass of N) ratio. Data obtained from https://doi.org/10.25921/zqwr-at45.

Station	Depth (m)	Temp	Sal	>5 phi (%)	Sed Chl a (mg/m^2)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	TOC (%)	C:N
CL1	41	7.47	31.70	75.93	7.13	-23.50	6.60	1.09	8.74
CL3	42	4.73	32.14	97.19	12.21	-22.20	7.60	1.24	6.94
DBO3-6	54	4.18	32.60	70.11	17.38	-21.50	7.20	1.04	6.41
DBO3-8	44	3.82	32.75	74.65	16.42	-21.20	7.80	1.08	6.23
ML1-5	37	5.59	31.70	36.84	7.60	-24.40	7.70	0.46	4.01
ML1-11	38	0.10	32.40	80.28	5.48	-22.50	9.50	1.02	6.48
ML1-13	42	-0.14	32.38	92.85	7.58	-22.60	9.80	1.12	6.01
ML3-6	42	-1.19	32.27	63.43	14.45	-22.90	7.00	1.00	7.57
ML3-10	36	0.71	32.21	50.14	12.53	-22.00	7.40	0.65	7.05
ML3-14	40	1.63	32.23	93.09	13.73	-22.10	7.60	0.98	7.18
ML4-9	36	-1.44	32.14	67.34	11.10	-22.20	7.40	0.87	6.72
ML4-14	44	-1.15	32.48	94.58	16.59	-21.90	8.10	1.35	6.75
ML6-1	30	5.88	31.03	17.55	6.14	-23.20	4.80	0.25	6.52
ML6-11	46	-1.66	32.47	73.95	9.97	-22.70	7.60	0.95	7.16
ML6-3	29	7.82	30.92	7.56	5.98	-23.50	4.40	0.15	6.23

2.8 Literature

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Chapter 3: The Arctic Chukchi Sea food web: simulating ecosystem impacts of future changes in organic matter flow[3]

3.1 Abstract

The Chukchi Sea continental shelf is a highly productive inflow shelf of the Arctic Ocean that is experiencing warming events and declines in seasonal sea ice cover at one of the fastest rates compared to other Arctic shelves. Climate-induced changes in phytoplankton and ice-algal production, inflow of terrestrial matter through riverine discharge and coastal erosion, and increases in bacterial production are all predicted to cause shifts in the composition and distribution of organic matter supply and energy flow in this system. The goal of this study was to examine potential shifts in the Chukchi Sea ecosystem under various future climate scenarios. To assess these goals, an existing Chukchi Sea ecosystem model by Whitehouse and Aydin (2016) by was updated by incorporating terrestrial matter as a food source, especially for benthic consumers. Incorporation of a terrestrial matter component allowed us to adjust phytoplankton biomass to better match recent measurements and to update the system-wide mass-balance. We also modeled potential impacts of climate-driven alterations in the composition and flow of organic matter supply on major ecosystem groups for the 2015 – 2050 period. Iterations showed that higher retention of phytoplankton biomass in the pelagic realm would depress biomass of most benthic-feeding organisms across several larger ecosystem groups (invertebrates, fishes, mammals). However, simulated increases in terrestrial matter inflow and increases in bacterial biomass had the potential to compensate for some of the reductions in the energy supply from phytoplankton to the benthic food web, as well as to diversify the supply in organic matter to the seafloor. This diversification could make the ecosystem more stable to future climate-driven changes.

Keywords: Ecosystem modelling, Ecopath with Ecosim, benthic food webs, terrestrial matter, bacterial production, future Arctic

3.2 Introduction

The Chukchi Sea continental shelf is one of the most productive Arctic shelves (Codispoti et al., 2013); however, patterns in primary productivity and subsequent flow of energy through the Arctic food web are being altered by the rapid warming and decline in seasonal sea ice cover (Steele et al., 2008;

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Serreze et al., 2009; Frey et al., 2015). Under past conditions of extended seasonal ice cover, up to 70 % of ice-associated and pelagic primary production was exported to the benthos through tight pelagic-benthic coupling, supporting high benthic invertebrate biomass (Grebmeier et al., 1988; Walsh et al., 1989). The high standing stock of benthic invertebrates in the Chukchi Sea supports many benthic-feeding higher trophic levels, e.g., spectacled eiders (*Somateria fischeri*), walruses (*Odobenus rosmarus*), and gray whales (*Eschrichtius robustus*) (Grebmeier et al., 1988; Lovvorn et al., 2003; Dehn et al., 2006; Moore and Huntington, 2008). Changes in atmospheric forcing and sea ice cover can have major impacts at the base of the Arctic food web, including levels of sea ice and phytoplankton production, the strength of pelagic-benthic coupling, and the importance of additional food sources, such as terrestrial matter inflow and temperature-dependent activity of bacterial communities (Bopp et al., 2001; Lavoie et al., 2010; Holmes et al., 2016; Taylor et al., 2018; Chapter 1). These changes may have repercussions for the energy flow between trophic levels. Ecosystem models are effective tools to evaluate the potential impacts of changing conditions on the energy flow through a system (e.g., Aydin and Mueter, 2007; Gaichas et al., 2011; Doney et al., 2012; Harvey et al., 2012). Current ecosystem models describe the Chukchi Sea ecosystem as a benthos-dominated system, where much of the primary production is routed through the benthos to higher trophic levels (Christensen and Walters, 2004; Aydin et al., 2007; Whitehouse et al., 2014; Whitehouse and Aydin, 2016); here, we offer perspectives on how changes in primary producer carbon supply and energy flow through the food web may impact the Chukchi Sea ecosystem.

In Arctic shelf systems, such as the Chukchi Sea, the benthos represents a cornerstone of the food web (Grebmeier et al., 1988; Aydin et al., 2007; Whitehouse et al., 2014). As organic matter sinks to the seafloor, benthic organisms utilize this material directly as food, as well as indirectly affect the detrital distribution and mineralization into nutrients via respiration and bioturbation activities (Heip et al., 1995). The standing stock of the benthic community largely depends on the amount and quality of the detrital material fulfilling the energetic needs of the community (Gooday et al., 1990; Ruhl and Smith, 2004). The reliance of benthic organisms on different organic matter sources (such as from bacteria, phytoplankton, and terrestrial) is variable (Chapter 2), and changes in the composition of organic matter to the seafloor can have implications to the benthic community composition. These changes can in turn affect ecosystem processes and the strong food web connections dependent on the Arctic benthos (Węsławski et al., 2011; Kędra et al., 2015).

Ice-algal and phytoplankton production is typically considered the main food source for the Arctic benthos. Sea ice modulates the amount of light that is available for photosynthesis, as well as the timing

and stratification depth of the surface ocean through control of mixing and heat transfer (Woodgate et al., 2006; Brown and Arrigo, 2013). In climate situations with abundant seasonal sea ice, the seasonal increase of light and ice melt in late spring results in early-season ice-edge blooms, often dominated by centric diatoms, that sink rapidly and largely ungrazed to the benthos (Grebmeier and McRoy, 1989; Lovvorn et al., 2005). With a reduction of sea ice in warmer years, the ice-algal production is reduced and phytoplankton blooms tend to occur later in a thermally stratified water column (Wassmann and Reigstad, 2011). Increased light availability and a longer growing season in ice-free conditions allows for overall increased Arctic primary production (Brown and Arrigo, 2013). However, a shift towards smaller-celled phytoplankton communities (Li et al., 2009; Morán et al., 2010) and an increase in grazing pressure by zooplankton (Neeley et al., 2018) likely results in higher proportions of primary production being retained in the water column. Such a shift would lead to a weakening of pelagic-benthic coupling in the system with strong impacts on the benthos-dependent food web (Lalande et al., 2007; Arrigo et al., 2008; Wassmann and Reigstad, 2011).

Organic matter sources, other than ice algae or phytoplankton, that support the benthic food web on the Chukchi shelf, include terrestrial matter and bacteria. Carrying terrestrial matter, Arctic river discharge has increased by 2.6 % per decade since the 1970s (Bopp et al., 2001; McClelland et al., 2006; Lantuit et al., 2012) due to increases in coastal erosion and permafrost thaw (Guo et al., 2004; Semiletov et al., 2011). The presence of terrestrial matter in Chukchi Sea marine sediments and invertebrate diets is high, illustrating the importance of this material to the benthic food web in this region (Yunker et al., 2005; Morris et al., 2015; Chapter 1, Chapter 2). Although the input of terrestrial matter via rivers and coastal erosion is typically still smaller than the input from marine primary producers, even in a warming climate, an increases of terrestrial material could affect the direction and efficiency of energy flow through the food web (Dunton et al., 2006). Additionally, bacteria contribute nutritional value to the detrital food supply to consumers and also play an important role in the breakdown and recycling of organic matter (e.g., Newell, 1965; Heip et al., 1995). While Arctic bacterial production and metabolic processes are well adapted to the ambient low temperatures, the predicted increases in bottom water temperature on the Chukchi shelf (Wang et al., 2012) are likely to result in higher bacterial metabolic processes and production (Pomeroy and Deibel, 1986; Kirchman et al., 2009; Chapter 2). This could lead to changes in the carbon cycling of the system, and a potential increase in the importance of bacteria as a food source, especially in benthic food webs (Kirchman et al., 2009; McMeans et al., 2013; Bell et al., 2016). Therefore, both terrestrial and bacterial sources should be considered in predictive ecosystem models of the Chukchi Sea.

The goal for this study was to enhance our understanding of trophic pelagic-benthic couplings in the Chukchi Sea ecosystem, and to examine potential ecosystem shifts under future climate scenarios. To address these goals, a recent Chukchi Sea ecosystem mass-balance model (Whitehouse and Aydin, 2016) was updated to include terrestrial matter as a potentially important food source. We determine the necessary terrestrial biomass to balance the ecosystem model with a loss in phytoplankton derived organic matter. We accordingly re-defined the routing of phytoplankton, terrestrial, and bacterial matter through the benthic food web. This updated model was then used to determine potential impacts of climate driven variability in organic matter supply to the food web over time. We hypothesize that weakening of pelagic-benthic coupling would negatively impact benthic biomass and benthos-dependent trophic pathways, but that an increase in terrestrial material and bacterial production would compensate for some of the loss of phytoplankton-derived detritus to the benthos-driven food web.

3.3 Materials and Methods

3.3.1 Study area

The Chukchi Sea is a shallow (~ 50 m max), marginal, highly productive shelf of the Arctic Ocean bounded by the Alaskan and Siberian coasts (Fig. 3.1). Three major water masses (Bering Shelf Water, Anadyr Water, and Alaska Coastal Water) flow through the Bering Strait northward and spread across the shelf (Coachman et al., 1975). Bering Shelf and Anadyr waters mix once on the shelf into the salty (30.0 - 33.5), cold (0 – 7 °C), and nutrient-rich Bering Shelf Anadyr Water that flows northwards through the central channel of the Chukchi Sea. Alaska Coastal Water is a nutrient-poor and freshwater-influenced (salinity 20 – 32, 7 - 12°C) water mass that flows along the eastern coast of the Chukchi Sea that carries terrestrial matter from the Yukon River. The Yukon River discharges about 2×10^{11} m^3 freshwater and 2.02×10^{12} g total organic carbon annually into the Bering Sea (Guo and Macdonald, 2006), much of which is advected onto the Chukchi shelf (Coachman, 1986; Jorgenson and Brown, 2004; Guo and Macdonald, 2006; Pisareva et al., 2015). The Chukchi shelf is sea ice covered for up to 7 months a year (November – May), resulting in short seasonal pulses of ice edge-associated primary production (Walsh et al., 1989). Variations in physical properties and biological dynamics, such as timing and location of phytoplankton blooms, grazing pressure of zooplankton, and organic matter degradation through microbes, have strong influences on the amount of pelagic-benthic coupling and organic matter pathways in the Chukchi Sea (Walsh et al., 1989; Grebmeier and Barry, 1991).

Modeling Approach

1. *Ecopath modelling framework*

Ecopath (http://ecopath.org/) is a publicly available ecosystem modeling software package that allows the user to create a mass-balanced snapshot of a system of interest. Configuration of the model requires categorization of the organisms, or groups of organisms, that will be represented and information about how these groups are related though energy flow. The model summarizes and optimizes information on biomass, diet composition, rate of production and consumption, biomass removals from fishery and natural mortality, and information about detrital fate (Christensen and Pauly, 1991; Christensen et al., 2000). Ecopath is based on the assumption of steady state mass-balance over an arbitrary period of time, in this study, a year. The program uses two governing equations, describing both the production and energy balance of each organismal compartments, or functional group. These equations quantify the material (biomass) moving in and out of functional groups in a given food web. A functional group can consist of a single species, a set of species, or represent a detrital pool. Following are the master equations in Ecopath, for each functional group (i) (or box):

$$P_i = Y_i + B_i * M2_i + E_i + BA_i + P_i(1 - EE_i) \qquad (1)$$

Production = fisheries catch + predation mortality + biomass accumulation + net migration + other mortality

$$(Q/B)_i * B_i = \left(\frac{P}{B}\right)_i + B_i + R_i + UN_i \qquad (2)$$

Consumption = production + respiration + unassimilated food

Definitions of the parameters in the two equations are given in Table 3.1.

Model parameters can be specified based on observational data, experimental results, or estimated by the model by solving the set of equations. While most parameters are mandatory inputs, the parameters biomass (B), consumption to biomass ratio (Q/B), production to biomass ratio (P/B), and ecotrophic efficiency (EE) are optional, as they can be computed by Ecopath given all other parameters. Ecopath links the production of each functional group with the consumption of all other groups and uses the linkages among groups to estimate any missing parameters, using one equation for each functional group. Ecopath works with energy-related currencies and energy output and input must be balanced, so that production of any group is routed to other functional groups within the system, or out of the system.

If not balanced, the EE of a group is >1, indicating that less material is entering the group or box than is consumed. In this study, all production terms represent annual integrations.

2. Update of existing mass-balance model

The most recent version of Ecopath model for the eastern Chukchi Sea shelf, along with the parameter values, were acquired (Whitehouse and Aydin, 2016) (Table 3.2) and used as baseline model. In the present study, phytoplankton biomass was then reduced to reflect best estimates of annual production on the Chukchi Sea shelf (Arrigo and van Dijken, 2015), terrestrial production was added to account for external organic matter input and balance the reduction in phytoplankton biomass, detrital fates were adjusted to account for the export of material (e.g., waste products) to both terrestrial and phytoplankton detritus pools, and diets of benthic invertebrates were adjusted to reflect our recent findings (Chapter 2) (Table 3.3, Fig. 3.2).

i. Phytoplankton

In the development of the original model, a top-down balance approach was used to estimate phytoplankton production in the system resulting in an annual phytoplankton production of ~170 g C m^{-2} y^{-1} for the original Chukchi Sea model (Whitehouse et al., 2014). This was later adjusted closer to empirical values by Whitehouse and Aydin (2016) to an annual phytoplankton production of 141 g C m^{-2} y^{-1} by reducing phytoplankton biomass from 27.8 t km^{-2} to 15.0 t km^{-2}, assuming a P/B ratio of 75 and 150 days of growing season for phytoplankton. Whitehouse and Aydin (2016) acknowledged that these annual production and biomass values were still high but were needed to balance an insufficient supply of phytoplankton biomass to the benthic detritus box. Annual primary production estimates for the Chukchi shelf are highly variable, ranging from 20 g C m^{-2} to >400 g C m^{-2} y^{-1} (Sakshaug, 2004), but an average annual primary production of ~141 g C m^{-2} y^{-1} for the entire shelf is likely an overestimate. Annual primary production estimates for the shelf in recent years were closer to ~96 g C m^{-2} y^{-1} (Arrigo and van Dijken, 2011), about 30 % lower than the Whitehouse and Aydin (2016) model requires. To reflect these findings, phytoplankton biomass was reduced by 30 % to 15.0 t km^{-2} in our updated model while keeping P/B values at 75, assuming an average growth rate for Arctic diatoms to be ~0.5 d^{-1} (Connell et al., 2018) and a growing season of ~150 days (Walsh et al., 1989).

ii. Detrital components

Terrestrial organic matter was not included as a food source in any of the previous mass balance Chukchi Sea ecosystem models (Aydin et al., 2007; Whitehouse, 2013; Whitehouse et al., 2014; Whitehouse and Aydin, 2016). For our updated model, a novel terrestrial production box was added to reflect the terrestrial organic matter that is imported onto the shelf as detritus, where it serves as a food source for the benthic food web. The P/B value for terrestrial production was set to 75, assuming a similar growth rate and 150-day growing period as marine primary producers. The value of 'terrestrial production' biomass was then estimated in an iterative process, starting at 10 t km^{-2}, until the model was balanced (see: Model balancing).

Chukchi Sea benthic invertebrates were permitted to utilize terrestrial matter and bacteria in our updated model in addition to phytoplankton based on our recent findings (Chapter 2). In the original model (Whitehouse and Aydin, 2016), benthic invertebrates largely fed on benthic detritus, a functional component fueled by inputs from primary pelagic production and secondary production including molts and fecal pellets. For a finer delineation of detrital sources in our updated model, we created a component of phytoplankton production that was retained in the pelagic system (phytoplankton retained detritus) and one where phytoplankton was exported to the benthos (phytoplankton export detritus). The phytoplankton export detritus component replaced the 'benthic detritus' box of the original Whitehouse and Aydin (2016) model.

iii. Detrital fate

In our updated model, the phytoplankton export detritus component received ~70 % of phytoplankton production, while the remaining 30 % was routed into the phytoplankton retained detritus component. All non-assimilated matter by consumers, e.g., through excretion and other processes, was routed in equal amounts to the phytoplankton retained detritus component and the terrestrial detritus component. These proportions are consistent with those used in the Whitehouse and Aydin (2016) model, although in that model all detrital material from non-assimilated food and waste products was routed into the benthic detritus box (Fig. 3.2). As in the original Whitehouse and Aydin (2016) model, we also assumed that benthic invertebrates directly utilized benthic bacterial biomass, and parameters for this benthic bacterial box remained unchanged. Finally, detrital flux from fishery discards (in the Chukchi Sea this is related to subsistence harvests) was routed equally into phytoplankton export and terrestrial detritus components.

iv. Consumer diets

Diets of all functional groups within the original Whitehouse and Aydin (2016) model were set at a fixed diet proportion from detrital sources or prey component. In our updated model, diets of all benthic invertebrates were adjusted based on recent findings that determined the proportions of bacterial, phytoplankton, and terrestrial matter in Chukchi Sea benthic invertebrate diets (Chapter 2). Specifically, the diets of the following benthic invertebrate groups were updated based on the following species from Chapter 2: snow crab (*Chionoecetes opilio)*, shrimp (average of *Argis* and *Eualus*), benthic amphipod (*Anonyx*), Bivalvia (average of *Serripes*, *Macoma*, and *Nuculana*), Gastropoda (*Buccinum*), Polychaeta (Maldanidae), and worms etc. (containing bryozoans) (*Alcyonidium*). A mean of all decapod diets (*C. opilio*, *Argis*, *Eualus*) was used for the box "other crabs" (see Table 3.3). Other benthic invertebrate boxes in the model were updated using a mean of the proportional diet contributions of the three organic matter sources across all benthic taxa from Chapter 2, spanning a multitude of taxonomic groups and feeding characteristics. Diets of pelagic invertebrates, such as Cephalopoda and jellyfish were not updated from those used previously (Whitehouse and Aydin, 2016). In the original Whitehouse and Aydin (2016) model, benthic bacteria were assumed to obtain 100 % of their diet from 'benthic detritus'. Because 'benthic detritus' in our updated model was split into terrestrial detritus and phytoplankton export detritus, benthic bacteria were assumed to consume equal amounts of these two pools. The diets of all higher trophic levels (fish, birds, marine mammals) were kept the same as in Whitehouse and Aydin (2016).

v. Model balancing

Once updated, the model needed to be re-balanced based on the reduced phytoplankton production and the added terrestrial production. Because phytoplankton production was set, balancing was achieved by adjusting terrestrial production in a stepwise fashion, increasing production values in 0.1 t km^{-2} increments until the model was in balance (following procedures in Whitehouse and Aydin, 2016).

3. Ecosim framework

Once the updated mass-balanced Ecopath model for the Chukchi Sea was balanced, we used Ecosim to run dynamic simulations of the model (Walters et al., 1997; Christensen et al., 2000; Walters et al., 2000). Ecosim allows for the manipulation of parameters and analysis of potential impacts of a changing environment on the food web. Ecosim is expressed through a master equation derived from the Ecopath equations (eq. 1 and 2) as follows:

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (MO_i + F_i + e_i)B_i \qquad (3)$$

Definitions of the parameters in the equation are given in Table 3.1.

Ecosim provides the ability to adjust different parameters in a given model over time, including forcing of biomass of specific components at the base of the food web such as phytoplankton or detrital sources. Ecosim only describes feeding interactions, and changes in model parameters will affect biomass of the respective functional groups. For the purpose of this study, our updated Ecopath model is assumed to define steady state conditions. Then, changes over the 2015-2050 period were cumulatively applied to phytoplankton production, strength of pelagic-benthic coupling, terrestrial matter inflow, and bacterial production (simulations 1-4 below), meaning each subsequent simulation also included the changes of all previous simulations.

4. Model simulations to explore impacts of environmental change

i. Detrital biomass

Ecosim simulations require detrital biomass to be entered directly. The biomass of detrital pools reflects the sum of non-assimilated food and organic matter flows from other mortality divided by the P/B ratio of the detritus pool in question:

$$Detritus\ biomass = \frac{\left(\frac{B * Q}{B * UN}\right) + \left(\frac{B * P}{B[1 - EE]}\right)}{P\frac{P}{B}_{detritus}} \quad (4)$$

The P/B ratio in this case is expressed as 1/turnover and reflects the turnover time of detritus. In systems with slow turnover, such as the Arctic, the P/B ratio is usually assumed to be low. Here, we assumed a P/B ratio of 0.5 as a general, intermediate value, which is fast enough to show some detrital dynamics, but slow enough to be stable and reflect detrital burial (Christensen and Pauly, 1993; A. Whitehouse. pers. comm). The sum of flows to each detrital pool was calculated and entered into the basic input in Ecopath.

ii. Simulation 1: Increased phytoplankton biomass

The continued reduction in sea ice cover on Arctic shelves may lead to an increase in phytoplankton production by 10 % between 2015 and 2050 (Arrigo and van Dijken, 2015). To represent a ~10 % increase in phytoplankton production for this simulation, we assumed a linear annual 0.28 % increase in phytoplankton biomass over the targeted time frame (2015-2050), from an initial phytoplankton biomass of 15.0 t km^{-2} in 2015 to 16.5 t km^{-2} by 2050.

iii. Simulation 2: Weakening of pelagic-benthic coupling

Phytoplankton communities are expected to shift to smaller phytoplankton species and an increase in zooplankton grazing on pelagic production is predicted to result in a decrease in the flux of pelagic production to the seafloor (Lalande et al., 2007; Arrigo et al., 2008; Wassmann and Reigstad, 2011). To reflect this change, we assumed in this simulation, in addition to increased phytoplankton biomass (simulation 1), that 30 % rather than 70 % of primary production as in the steady state model is routed to the seafloor; conversely, 70 % of phytoplankton biomass rather than 30 %, as in the steady state model remains in the pelagic realm.

iv. Simulation 3: Increase in terrestrial matter inflow

Increased river discharge and coastal erosion are expected to increase the influx of terrestrial matter onto the Chukchi Sea shelf (Semiletov et al., 2011). In this simulation, in addition to the increase in phytoplankton production and a weakening in pelagic-benthic coupling (simulations 1 and 2), we assumed that terrestrial matter loading will increase in proportion to the predicted increase of river discharge of 2.6 % per decade (Bopp et al., 2001; McClelland et al., 2006). Accordingly, terrestrial biomass was increased at a linear rate (0.26 % y^{-1}) over 35 years (2015-2050) from an initial biomass value of 15.6 t km^{-2} (see results) to a final value of 29.7 t km^{-2}.

v. Simulation 4: Increase in bacterial production

Bacterial production in Chukchi Sea sediments at 5 °C increased by 182 % within 12 h relative to bacterial production at ambient 0 °C under replete substrate conditions (Chapter 1). To reflect this response to warming temperatures, in this simulation, we assumed a linear increase of 182 % in benthic bacterial biomass to represent an increase in bacterial production between 2015 and 2050, so that bacterial biomass increased from an initial value of 26.4 t km^{-2} to 74.4 t km^{-2}. Previous model adjustments, i.e., the increase in phytoplankton production, a weakening in pelagic-benthic coupling, and an increase in terrestrial matter inflow (simulations 1 and 2) were also applied.

3.4 Results

Changes in detrital sources at the base of the food web

In our updated model, major changes at the base of the food web (Fig. 3.3) were the reduction of phytoplankton biomass entering the model and the addition of terrestrial detritus (Fig. 3.2). Following the reduction of phytoplankton biomass, the model was initially out of balance due to a higher demand

for detritus than the model provided (EE>1 for phytoplankton export detritus). After the addition of a terrestrial detritus component and updates to diets of benthic invertebrates, the phytoplankton export detritus component was balanced, but the overall model was still out of balance due to insufficient supply of terrestrial detritus (EE>1 for terrestrial detritus). Therefore, terrestrial detritus was increased in 0.1 t km^{-2} increments until the model was in balance at 15.6 t km^{-2} (EE<1 terrestrial detritus).

The throughput representing the size of the entire system in terms of matter flow was calculated by Ecopath directly as 9277.5 t km^{-2} yr^{-1} in the updated model, compared to 8453.1 t km^{-2} yr^{-1} in Whitehouse and Aydin's (2016) model. Most updated model components (mammals, birds, fish, pelagic invertebrates) exhibited similar biomass to that of the Whitehouse and Aydin (2016) model. Adjustments to phytoplankton production values, and the addition of terrestrial detritus, resulted in decreases of overall production of phytoplankton (from 2085 to 1125 t km^{-2} yr^{-1}) and slight increases in microbial production (from 625 to 730 t km^{-2} yr^{-1}) (Fig. 3.4). While these changes did not lead to strong changes in biomass of the consumer components of the model, energy flow in our updated model was more diversified with the addition of more detrital groups.

Model simulations

Outputs from model simulations are presented as relative biomass. Relative biomass refers to the change in biomass of a certain ecosystem group relative to the initial biomass of that group at the beginning of the simulation period. Model results show change in relative biomass at the end of the model simulation period (2050) for major ecosystem groups (Fig. 3.5a-d). An increase in phytoplankton production (simulation 1, Fig. 3.5a) resulted in slight increases of relative biomass across all ecosystem groups, ranging from 1 to 18 %. The largest increase in relative biomass was observed in pelagic invertebrates, with a relatively narrow spread among their functional groups (12-18 %; Appendix 1). Smaller increases in relative biomass occurred in birds and fishes, while benthic invertebrates and marine mammals remained practically unchanged in average relative biomass. Within these ecosystem groups, largest biomass increases were typically observed in pelagic-feeding functional groups, such as pelagic-feeding birds versus piscivorous birds (see Appendix 1).

When the system was forced into a state of weakened pelagic-benthic coupling in addition to phytoplankton biomass increases (simulation 2, Fig. 3.5b), average relative biomass increased in pelagic invertebrates and birds, but decreased in benthic invertebrates, benthic fishes, and benthic marine mammals. Relative biomass of pelagic invertebrates increased most (average 26 %) with the enhanced

retention of primary production in the pelagic realm. A more variable response was observed in birds, where relative biomass of planktivorous birds (e.g., scolopacids) increased (between 24-32 %), while most piscivorous birds remained stable or decreased in biomass by up to 6 % (e.g., larids, cormorants). The strongest declines in biomass were observed in benthic invertebrate groups (9-68 %, average 27 %) with especially large declines for groups that fed on a variety of organic matter sources (Appendix 1b). Fishes showed the largest range in responses with increases in biomass by up to 36 % in some of the pelagic-feeding groups, especially Arctic cod (*Boreogadus saida*), salmon (Salmonidae), and pollock (*Gadus chalcogrammus*), and decreases in relative biomass in mostly benthic-feeding groups, such as small-mouth flatfish (*Etropus microstomus*), sculpins (Cottoidea), and skates (Rajidae) (between 17-47 % decrease). Particularly benthic-feeding mammals, including gray whales (*Eschrichtius robustus*), Pacific walrus (*Odobenus rosmarus*), and bearded seals (*Erignathus barbatus*) experienced decreases in biomass ranging from 18 to 26 %.

An increase in terrestrial organic matter inflow onto the shelf, in addition to increased phytoplankton production and weakened pelagic-benthic coupling (simulation 3, Fig. 3.5c), resulted in small increases in relative biomass of most groups, compensating for several of the biomass declines observed in simulation 2. Relative biomass of pelagic invertebrates was similar to that in previous simulations, indicating that this ecosystem group was mostly unaffected by the terrestrial matter influx (Appendix 1a). Equally, average bird biomass in simulation 3 was similar to levels in simulation 2 but with no functional group experiencing a decrease. Benthic invertebrates, on average, showed a small increase in relative biomass compared to the steady state level and simulation 2 responses, albeit with a large range among functional groups. Benthic invertebrate functional groups that showed the largest increases in biomass were snails, benthic urochordates, and sponges (increases by 60 %, 44 %, and 43 %, respectively), while decreases in relative biomass were observed in, e.g., snow crab (*Chionoecetes opilio*) (-17 %) (Appendix 1b). Fishes showed a similar trend as benthic invertebrates with minor increases compared with the steady state level and higher average biomass compared with the previous simulation. Largest biomass increases in fishes (up to 33 %) occurred in mostly pelagic-feeding species, but some benthic-feeding fishes also experienced declines in biomass (up to -10 %). Average marine mammal biomass remained unchanged compared to steady state conditions with largest increases in biomass observed in pelagic-feeding mammals (+18 %).

Lastly, an increase in bacterial production resulted in large average biomass increases in all ecosystem groups, except pelagic invertebrates, but with a great range in functional groups within each

ecosystem group (simulation 4, Fig. 3.5d). Pelagic invertebrates remained mostly unaffected by the increase in bacterial production compared with previous simulations. Benthic invertebrates experienced the strongest increases in relative biomass, between 46 – 182 % for different functional groups (Appendix 1b). The second largest increase in biomass occurred in fishes, with strongest responses in benthic-feeding fish groups (up to 170 %, Appendix 1c). The simulated increase in bacterial production also resulted in higher relative biomass of up to 87 % in piscivorous birds, while it only increased in planktivorous birds by up to 32 %. Marine mammals responded with stronger biomass increases to enhances in bacterial production than to any prior simulation, with biomass increases of up to 90 % in some benthic-feeding species.

3.5 Discussion

Unprecedented changes occurring on Arctic shelves, such as the Chukchi Sea, have the potential to alter the supply of various organic matter sources to the benthos and influence the flow of energy through the ecosystem. In an effort to predict the potential food web responses to these changes, here we performed a series of model simulations with an updated Chukchi Sea ecosystem model (Whitehouse and Aydin, 2016). We found that the addition of terrestrial matter as a benthic food source diversified the energy flow at lower benthic trophic levels, but overall energy flow through the ecosystem components and biomass remained largely the same as in the previous model by Whitehouse and Aydin (2016). Further, cumulative model simulations of climate-driven changes in phytoplankton production, strength of pelagic-benthic coupling, terrestrial matter inflow, and bacterial production were used to assess potential changes in major ecosystem groups of the Chukchi Sea. Most ecosystem groups increased slightly in biomass with elevated phytoplankton production, while feeding habits (pelagic-feeding versus benthic-feeding) strongly influenced the changes in biomass in subsequent simulations. In several groups, high terrestrial inflow and increases in bacterial production had the potential to compensate for the loss in phytoplankton export to the benthos in a weakened pelagic-benthic coupling scenario.

Annual phytoplankton production in the original Chukchi Sea ecosystem model was estimated at ~141 g C m^{-2}, so that balanced energy flow through the functional groups could be established; however, the production value was considered an overestimation (Whitehouse and Aydin, 2016). This suggests that there are food sources in the system that were not included in the original model. One of these food sources could be terrestrial matter. Terrestrial matter has traditionally been assumed a negligible food source in Arctic marine food webs (Schell, 1983), but has recently been identified as a major contributor to Arctic benthic invertebrate diets (Dunton et al., 2006; Bell et al., 2016; Harris et al., 2018; Rowe et al.,

2019; Chapter 1). For example, ~40 % on average and up to 80 % at some locations of the organic matter in Chukchi Sea sediments can originate from terrestrial matter (Chapter 1). Some consumers like the benthic snail *Buccinum* derived on average 81 % of their diet from terrestrial sources on the shelf (Chapter 2). In our balanced model, 15.6 t km^{-2} of terrestrial organic matter were needed to sustain the high benthic biomass. This may be a high estimate of terrestrial carbon for the Chukchi Sea. Regional benthic carbon concentrations on the Chukchi shelf have been reported as 5.6 – 7.5 g m^{-2} (Naidu et al., 1993); assuming 40 % of this to be terrestrial matter (Chapter 1), this would at maximum amount to only about a fifth of the terrestrial carbon concentrations, that we calculated to balance the model. More in-depth analyses of terrestrial matter concentrations in sediments would improve our ability to model energy flux from the different food sources. However, this new model provides a new portfolio framework of the Chukchi Sea ecosystem, where a more diversified food base may present a more stable system than previously realized.

Arctic benthic invertebrates, especially detritivores, utilize a variety of organic matter sources deposited to the benthic environment. The use of terrestrial matter by benthic invertebrates has recently been confirmed across various regions of the Alaskan Arctic shelves (Bell et al., 2016; Harris et al., 2018; Rowe et al., 2019; Chapter 2), emphasizing the need to include terrestrial matter into ecosystem models for this region. Information about the proportional contribution of bacteria, phytoplankton, and terrestrial matter to the diets of ten common benthic invertebrate species on the Chukchi shelf, ranging across feeding types and taxonomic groups (Chapter 2), allowed for better resolution of detrital source use in our updated model. What is less well known at this point is the efficiency with which terrestrial matter can be assimilated by these invertebrates. In other areas, such as the Beaufort Sea, the utilization of terrestrial matter in benthic food webs increases the trophic steps in the system by reducing the trophic efficiency and the flow of energy to higher trophic levels (Dunton et al., 2006; Bell et al., 2016). Bacterial processes may break down terrestrial matter for better incorporation into marine food webs (Garneau et al., 2009), which increases bacterial production in regions of high terrestrial influx (Figueroa et al., 2016). Energetically, however, the added trophic level of bacterial processing can reduce overall energy transfer efficiency to higher trophic level consumers (Sommer et al., 2002; Berglung et al., 2007). For example, in boreal lake systems, terrestrial organic matter subsidies are abundantly used, but are less effective in supporting consumer population biomass than other food sources (Karlsson et al., 2015). Therefore, trophic transfer efficiency of terrestrial matter in the Chukchi Sea food web will need to be further investigated to understand the importance of terrestrial matter addition to the energy pathways in the updated model.

Ecosystem model simulations are a valuable tool to discern potential responses of various ecosystem components to anticipated changes in the energy supply and flow of a system. The large changes that Arctic shelf ecosystems are experiencing because of climate change (Steele et al., 2008; Serreze et al., 2009; Frey et al., 2015) make this a particularly valuable and tractable system for model simulations. Here, we implemented four simulations in a stepwise cumulative fashion, meaning that each subsequent simulation also contained the previous changes. In the natural system, complex ecosystem changes at the base of the marine food web and energy flow are unlikely to happen consecutively, but occur simultaneously and likely not linearly (Doney et al., 2012). However, to discern stepwise responses across the ecosystem, we applied an order where an increase in phytoplankton production (Arrigo and van Dijken, 2015) was followed by weakening of pelagic-benthic coupling (Lalande et al., 2007; Wassmann and Reigstad, 2011), because of greater retention of smaller phytoplankton cells in the water column (Li et al., 2009) and greater grazing pressure in the plankton (Neeley et al., 2018). This enhancement of the pelagic food web may then be countered by an increase in other food subsidies to the benthic system, namely terrestrial matter and subsequent increase of bacterial production (Bopp et al., 2001; Kirchman et al., 2009).

Reductions in sea ice cover allow for a longer growing season of pelagic production and have been estimated to increase by 10 % over the next 35 years (Simulation 1, Arrigo and van Dijken, 2015). Enhanced pelagic production resulted in slight increases in relative biomasses of all major ecosystem groups across all trophic levels, reflecting the larger carrying capacity of a more productive system (Christensen and Paul, 1998). The simulations in our model are only based on feeding interactions and do not take into account other aspects that add complexity to the simulation responses. For example, changes in the physical environment (e.g., warming, Grebmeier et al., 2006; Wang et al., 2012) may cause shifts in community composition that could alter the simulated response to enhanced primary production, which assumes constant community composition. Zooplankton community composition has shifted over the past decades due to larger proportions of Pacific zooplankton species entering the Chukchi shelf in the summer (Matsuno et al., 2011; Ershova et al., 2015) and trends towards smaller microzooplankton species during warm conditions (Dolan et al., 2014). Similar climate-driven changes have been found in the Atlantic Arctic, with increasing proportions of smaller copepod species due to changes in the phytoplankton community, temperature, and inflow of boreal species. Such changes in the zooplankton community could influence the efficiency with which the enhanced primary production is channeled through the food web though altered feeding rates, assimilation efficiencies, and lipid storage (Baier and Napp, 2003; Matsuno et al., 2011; Ershova et al., 2015). The increased retention of phytoplankton detritus

in the pelagic food web, and subsequent higher zooplankton biomass, may supply larger quantities of prey items to pelagic-feeding higher trophic level species such as Arctic cod. This, in turn, could lead to increased biomass that supports higher trophic level predators including seals, whales, and birds (Welch et al., 1992; Hop and Gjøsæter, 2013; Marsh et al., 2017). Although increased food availability could lead to increases in biomass in lower trophic levels, observed trends in zooplankton community composition suggest a shift towards smaller, less lipid-rich copepod species (Matsuno et al., 2011; Ershova et al., 2015), which suggests that subsequent energy transfer through the pelagic food web will eventually be reduced. In addition to possible shifts in energy flow, ice-dependent species, such as Arctic cod may be affected by habitat loss from climate-related changes independent of energy flow. Sea ice is an important habitat for Arctic cod juveniles for feeding as well as protection from predators (Geoffroy et al., 2011). Although Arctic cod responded positively to our simulated ecosystem changes, their likely temperature driven northward contraction and the survival of juveniles could impact the abundance of this key species in the Arctic food web with implications for higher trophic levels (Darnis et al., 2012). In addition, increased water temperatures are likely going to result in elevated metabolic demands by organisms.

The Chukchi Sea is known for its tight pelagic-benthic coupling exporting the majority of pelagic production to the benthos and supporting a rich benthic community. These communities serve as an important feeding ground for many higher trophic levels, including fish, birds, and mammals (Moore and Huntington, 2008). It is, therefore, unsurprising that a weakening in pelagic-benthic coupling (simulation 2) resulted in a strong decline of benthic invertebrate biomass due to the reduced amount of primary production reaching the seafloor in this scenario. In response to this reduction in benthic biomass, benthic-feeding marine mammals and fish showed strong declines in biomass (Gray et al., 2017; Jay et al., 2012; Moore and Gulland, 2014). For example, gray whales feed on a broad range of benthic invertebrates, but tend to primarily feed on ampeliscid amphipods (Yablokov and Bogoslovskaya 1984, Nerini 1984). The abundance and biomass of ampeliscids have declined in the Bering Sea, presumably due to changes in the primary production regime, although these changes could have resulted from top-down predation control (Coyle et al., 2007). An ampeliscid decline based on bottom-up factors would be in line with the simulated weakening in pelagic-benthic coupling and a subsequent decline in gray whale biomass and shifts of the foraging area of this top predator (Moore et al., 2003).

Increases in terrestrial organic matter source availability (simulation 3) could compensate for some of the biomass loss that several benthic groups experienced under the previous simulation scenario (simulation 2), depending on the composition of organic matter diet composition of benthic functional

groups. The addition of this terrestrial material to the model represents a diversification of food sources, which supports notions established for Arctic coastal systems that higher diversity of basal food sources stabilizes the overall food web (McMeans et al., 2013). Benthic functional groups that utilize high proportions of terrestrial matter (e.g., bivalves and sponges, Harris et al., 2018; Chapter 2) increased the most in relative biomass in a simulation of terrestrial matter addition, while benthic functional groups depending on high proportions of bacteria and phytoplankton in their diet decreased in relative biomass (e.g., snow crab, other crabs and benthic amphipods). Thus, the incorporation of detailed diet compositions in the updated model allowed us to identify some of the more vulnerable functional groups within the ecosystem to changes in the organic matter supply to the benthos rather than assuming mostly unified responses across all benthic invertebrates. A shift in food availability e.g., through increases in terrestrial organic matter influx could influence the organic matter availability changing the species composition in lower latitudes that are being exploited by higher trophic levels or counteract the influx of species into northern regions due to a diversification of food sources. For example, snow crab feeding mostly on bacteria and phytoplankton organic matter are already a common member of the Chukchi Sea benthic community (Bluhm et al., 2009; Divine et al., 2019; Iken et al., 2019), but are experiencing further northward shifts in abundance in the Bering Sea attributed to predation pressure and warming (Mueter and Litzow, 2008; Kolts et al., 2015). An additional shift in organic matter availability could further drive this species into higher latitudes. These results provide new context for potential distribution changes in benthic invertebrate species that are expected to occur in a warmer Arctic, as species composition drives foraging quality for higher trophic levels (Grebmeier and Dunton, 2000).

In addition to the incorporation of terrestrial matter as a food source, the increase in bacterial production further offset some of the expected biomass declines in response to a weakening in pelagic-benthic coupling. A decrease in pelagic production, and an increase in other organic matter subsidies, such as bacterial biomass, may change the habitat suitability for benthic invertebrates. Particularly vulnerable to such changes are benthic feeding organisms that rely heavily on phytoplankton organic matter sources e.g., some crabs, while those relying on bacterial matter would potentially thrive under increased bacterial organic matter availability (e.g., polychaetes, benthic amphipods). Food source availability could, therefore, influence the distribution of ecologically influential species and alter prey quality of the local community and change foraging areas for important predators (Alabia et al., 2018). Although biomass of all functional groups increased in this simulation, additional parameters can influence the strength of these effects. These can include temperature effects on growth rates and energy requirements, which will impact energy demands and flow through the system (Ambrose et al., 2006;

Bluhm et al., 2009; Węsławski et al., 2011). Higher temperatures could increase metabolic demands of all functional groups, giving rise to a higher demand for food supply, thus reducing the effects seen in our model simulations.

In conclusion, results from this study provided an updated model of the Chukchi Sea ecosystem, including new findings on organic matter supply and utilization. Changes in energy flow and diversification at the base of the Chukchi Sea food web provided a foundation to evaluate the response of major ecosystem components to the enhanced routing of energy through the pelagic or the benthic food web pathways. The loss in phytoplankton routing to the benthos in a weak pelagic-benthic coupling system may at least partially be offset by an increased inflow of terrestrial matter and in bacterial production. The effects of changes in pelagic or benthic energy flow were detectable throughout all trophic levels and taxonomic groups. However, other ecosystem changes, such as changes in competitive interactions from invading species, energetic composition of key prey items, or changes in trophic transfer efficiency of different organic matter sources, are likely to have effects across trophic levels, but were not reflected in the current model simulations. In future iterations, the model could be used to simulate other climate-driven changes, as well as potential future outside activities, including fishing and oil and gas extraction on the Chukchi shelf. The shelf is home to a variety of fish species and marine mammals that are an important subsistence resource for indigenous residents (Hovelsrud et al., 2008; Zeller et al., 2011). The model presented here is a useful tool to simulate potential changes in the system and manipulate parameters based on those activities (e.g., Harvey et al., 2012). This allows for the assessment of risks to targeted functional groups, guidance to stakeholders, and identification of knowledge gaps (Samhouri et al., 2009).

3.6 Acknowledgements

This publication was sponsored in part by the Cooperative Institute for Alaska Research with funds from the National Oceanic and Atmospheric Administration under cooperative agreement NA13OAR4320056 with the University of Alaska. This work was funded in particular through a National Ocean Partnership Program (NOPP grant NA14NOS0120158 to KI) by the National Oceanographic and Atmospheric Administration (NOAA), the Bureau of Ocean Management (BOEM) and Shell Exploration & Production under management of the Integrated Ocean Observing System (IOOS). SLD acknowledges support from the North Pacific Research Board's Arctic Integrated Ecosystem Program grants A91-99a and A91-00a to the Arctic Shelf Growth, Respiration, Advection and Deposition (ASGARD) rate experiments project. Thanks to Andy Whitehouse and Kerim Aydin for their continuous support in the development of this model. Additional thanks to Villy Christensen at the University of British Columbia for providing ACZ with the opportunity to attend the Ecopath class in Vancouver in 2017. We thank Matthew Wooller and Mary Beth Leigh (UAF) for valuable comments on this manuscript.

3.7 Figures and tables

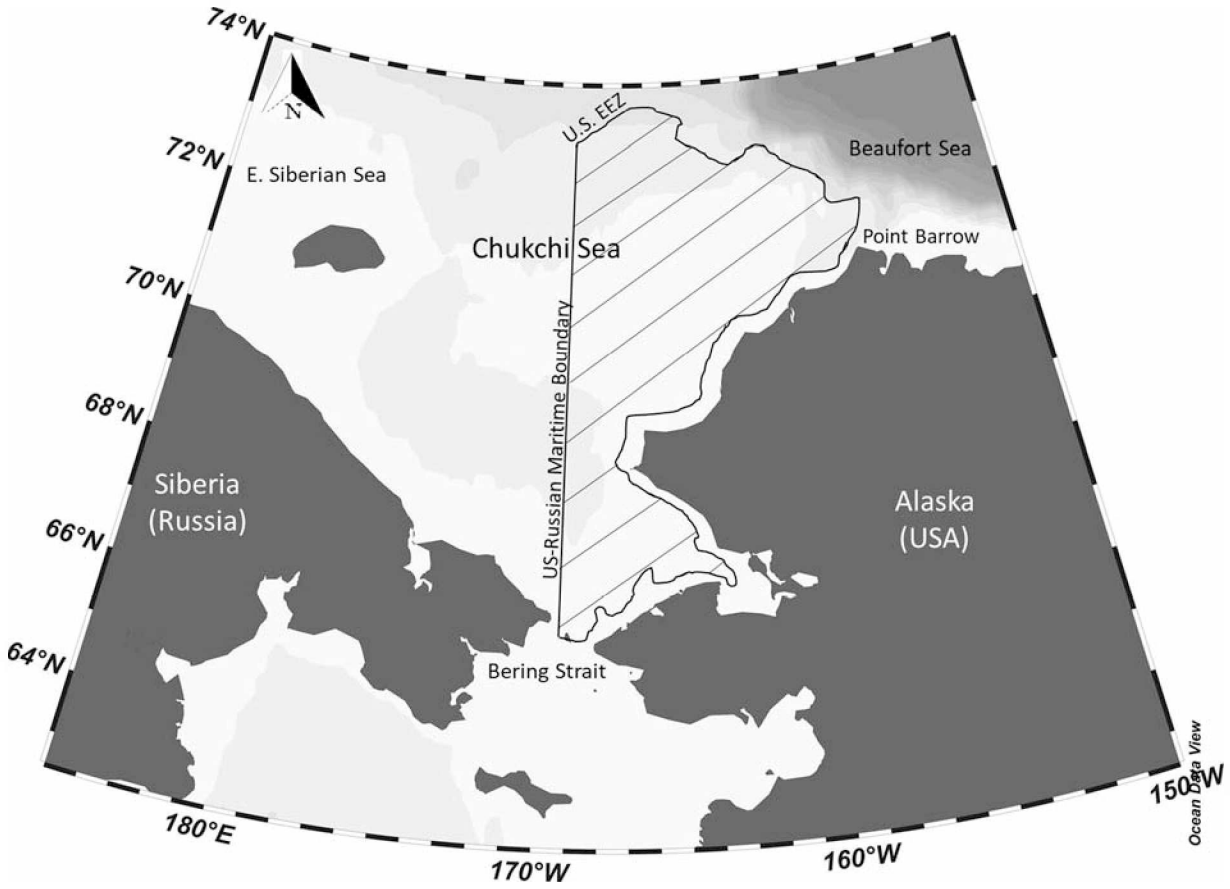


Figure 3.1: Map of the model area on the eastern Chukchi Sea shelf (hatched area). The model is bounded by the U.S.-Russia maritime boundary to the west, Bering Strait to the south, Point Barrow to the east, and the U.S. exclusive economic zones along the shelf break to the north.

Table 3.1: Term, descriptions, and units of parameters required for mass-balanced ecosystem model master equations in Ecopath and Ecosim.

Term	Description	Unit
P	Total production rate	t km^{-2} yr^{-1}
Y	Total fishery catch rate (here subsistence harvest)	t km^{-2} yr^{-1}
B	Biomass	t km^{-2}
M2	Instantaneous predation rate	yr^{-1}
E	Net migration rate (emigration-immigration)	t km^{-2} yr^{-1}
BA	Biomass accumulation rate	t km^{-2} yr^{-1}
1-EE	Other mortality	proportion (unitless)
EE	Ecotrophic efficiency	proportion (unitless)
Q/B	Consumption/biomass ratio	yr^{-1}
P/B	Production/biomass ratio	yr^{-1}
R	Respiration of group	t km^{-2} yr^{-1}
UN	Unassimilated food	proportion (unitless)
g	Gross food conversion efficiency (estimated as P/Q ratio)	unitless
Q	Total consumption rate	t km^{-2} yr^{-1}
I	Immigration rate	t km^{-2} yr^{-1}
MO	Instantaneous 'other mortality' rate	yr^{-1}
F	Instantaneous fishing mortality rate	yr^{-1}
e	Emigration rate per unit biomass	t km^{-2} yr^{-1}

Table 3.2: (Next page). Basic model parameters for the updated Ecopath model for the Chukchi Sea. Parameter inputs into the model were taken from Whitehouse and Aydin (2016). Parameters in bold were computed by the updated model. New functional groups and changed input parameters are highlighted by gray background. TL is trophic level, B is biomass (t km^{-2}), P/B is production to biomass ratio (y^{-1}), Q/B is consumption to biomass ratio (y^{-1}), EE is ecotrophic efficiency, GE is growth efficiency (y^{-1}), UN is unassimilated food, PED is phytoplankton export detritus, TD is terrestrial detritus, and PRD is phytoplankton retained detritus.

Table 3.2: continued.

	Group name	TL	B	P/B	Q/B	EE	GE	UN	PED	TD	PRD
1	Beluga	4.6	0.012	0.112	14.504	**0.211**	**0.008**	0.2	0.35	0.35	0.3
2	Gray whale	3.6	0.188	0.063	8.873	**0.000**	**0.007**	0.2	0.35	0.35	0.3
3	Bowhead whale	3.5	0.398	0.010	5.260	**0.299**	**0.002**	0.2	0.35	0.35	0.3
4	Polar bear Chukchi	5.3	0.0004	0.060	4.001	**0.663**	**0.015**	0.2	0.35	0.35	0.3
5	Polar bear S Beaufort	5.3	0.0001	0.060	4.001	**0.304**	**0.015**	0.2	0.35	0.35	0.3
6	Pacific walrus	3.4	0.059	0.069	21.662	**0.757**	**0.003**	0.2	0.35	0.35	0.3
7	Bearded seal	3.6	0.039	0.075	12.941	**0.912**	**0.006**	0.2	0.35	0.35	0.3
8	Ringed seal	4.5	0.056	0.088	19.228	**0.895**	**0.005**	0.2	0.35	0.35	0.3
9	Spotted seal	4.7	0.006	0.068	18.705	**0.385**	**0.004**	0.2	0.35	0.35	0.3
10	Procellarids	3.7	0.002	0.067	187.929	**0.000**	**0.0004**	0.2	0.35	0.35	0.3
11	Cormorants	4.3	0.000001	0.163	142.618	**0.000**	**0.001**	0.2	0.35	0.35	0.3
12	Scolopacids	3.5	0.0001	0.163	374.313	**0.000**	**0.0004**	0.2	0.35	0.35	0.3
13	Larids	4.5	0.0001	0.106	205.674	**0.000**	**0.001**	0.2	0.35	0.35	0.3
14	Alcids piscivorous	4.7	0.001	0.104	178.384	**0.741**	**0.001**	0.2	0.35	0.35	0.3
15	Alcids planktivores	3.5	0.0001	0.140	247.507	**0.000**	**0.001**	0.2	0.35	0.35	0.3
16	Large-mouth flatfish	4.1	**0.111**	0.401	1.780	0.800	**0.225**	0.2	0.35	0.35	0.3
17	Small-mouth flatfish	3.5	**0.090**	0.308	1.535	0.800	**0.201**	0.2	0.35	0.35	0.3
18	Large-mouth sculpin	4.1	**0.600**	0.400	2.000	0.800	**0.200**	0.2	0.35	0.35	0.3
19	Other sculpin	3.6	**0.855**	0.459	2.415	0.800	**0.190**	0.2	0.35	0.35	0.3
20	Eelpout	3.7	**0.382**	0.400	2.000	0.800	**0.200**	0.2	0.35	0.35	0.3
21	Pelagic forage fish	3.7	**1.191**	0.543	2.920	0.800	**0.186**	0.2	0.35	0.35	0.3
22	Misc. shallow fish	3.5	**6.498**	0.400	2.000	0.800	**0.200**	0.2	0.35	0.35	0.3
23	Other snailfish	3.8	**0.135**	0.400	2.000	0.800	**0.200**	0.2	0.35	0.35	0.3
24	Variegated snailfish	4.2	**0.099**	0.400	2.000	0.800	**0.200**	0.2	0.35	0.35	0.3
25	Alaska skate	4.1	0.005	0.210	**2.100**	**0.000**	0.100	0.2	0.35	0.35	0.3
26	Walleye pollock	4.1	0.001	0.869	3.008	**0.0001**	**0.289**	0.2	0.35	0.35	0.3
27	Pacific cod	3.8	0.00004	0.548	2.803	**0.744**	**0.195**	0.2	0.35	0.35	0.3
28	Saffron cod	3.8	**0.979**	0.548	2.803	0.800	**0.195**	0.2	0.35	0.35	0.3
29	Arctic cod	3.6	**1.045**	0.869	3.008	0.800	**0.289**	0.2	0.35	0.35	0.3
30	Salmon outgoing	3.5	0.001	1.280	13.560	**0.000**	**0.094**	0.2	0.35	0.35	0.3
31	Salmon returning	3.5	0.005	1.650	11.600	**0.027**	**0.142**	0.2	0.35	0.35	0.3
32	Cephalopoda	3.3	**0.011**	1.770	**8.850**	0.800	**0.200**	0.2	0.45	0.45	0.1
33	Bivalves	2.3	90.288	0.756	**3.778**	**0.029**	0.200	0.4	0.45	0.45	0.1
34	Snails	2.1	1.384	1.770	**8.850**	**0.060**	**0.200**	0.2	0.45	0.45	0.1
35	Snow crab	2.5	3.170	1.000	2.750	**0.082**	**0.364**	0.2	0.45	0.45	0.1
36	Other crabs	2.4	3.067	0.820	**4.100**	**0.187**	0.200	0.3	0.45	0.45	0.1
37	Shrimps	2.4	**7.492**	0.576	2.409	0.800	0.239	0.2	0.45	0.45	0.1
38	Sea stars	2.4	2.180	0.340	**1.700**	**0.014**	0.200	0.2	0.45	0.45	0.1
39	Brittle stars	2.4	5.644	0.485	**2.425**	**0.009**	0.200	0.4	0.45	0.45	0.1
40	Basket stars	2.4	0.510	0.340	**1.700**	**0.002**	0.200	0.2	0.45	0.45	0.1
41	Urchins, dollars, cucumbers	2.4	36.290	0.695	**3.475**	**0.007**	0.200	0.4	0.45	0.45	0.1
42	Sponge	2.2	0.527	1.000	**5.000**	**0.001**	0.200	0.4	0.45	0.45	0.1
43	Anemones	2.4	0.384	1.000	**5.000**	**0.361**	0.200	0.2	0.45	0.45	0.1
44	Benthic urchordate	2.2	1.160	3.580	**17.900**	**0.005**	0.200	0.4	0.45	0.45	0.1
45	Corals	2.4	0.003	0.046	**0.230**	**0.056**	0.200	0.4	0.45	0.45	0.1
46	Jellyfish	3.4	0.372	0.880	3.000	**0.002**	**0.293**	0.2	0.35	0.35	0.3
47	Benthic Amphipoda	2.6	**12.884**	1.000	**5.000**	0.800	0.200	0.4	0.45	0.45	0.1
48	Polychaeta	2.6	27.808	2.916	**14.579**	**0.035**	0.200	0.4	0.45	0.45	0.1
49	Worms etc.	2.4	17.040	2.230	**11.150**	**0.013**	0.200	0.4	0.45	0.45	0.1
50	Misc. crustaceans	2.4	5.581	2.008	**10.040**	**0.103**	0.200	0.4	0.45	0.45	0.1
51	Copepods	2.5	**1.951**	6.000	27.740	0.800	**0.216**	0.2	0.35	0.35	0.3
52	Other zooplankton	2.5	**1.168**	5.475	**15.643**	0.800	0.350	0.2	0.35	0.35	0.3
53	Pelagic bacteria	2.0	**1.421**	26.250	**75.000**	0.800	0.350	0.2	0.35	0.35	0.3
54	Benthic bacteria	2.0	**26.398**	26.250	**75.000**	0.800	0.350	0.2	0.45	0.45	0.1
55	Phytoplankton	1.0	15.000	75.000		**0.100**			0.7	0	0.3
56	Outside Terrestrial production	1.0	15.600	75.000		**0.000**			0	0.7	0.3
57	Phytoplankton export detritus	1.0	3944.760			**0.998**			0	0	0
58	Outside Terrestrial detritus	1.0	2821.520			**0.997**			0	0	0
59	Phytoplankton retained detritus	1.0	2173.080	0.500		**0.040**			0	0	0

Table 3.3: Proportional contributions of three organic matter sources (bacteria, phytoplankton, terrestrial) to benthic invertebrate functional groups in the Chukchi Sea based on data from Chapter 2. Table shows the functional groups in the model, organisms that were included in each functional group, and diet proportions. See text for details.

Functional group	Organisms included	Bacteria	Phytoplankton	Terrestrial
Snow crab	*Chionoecetes opilio*	0.498	0.360	0.142
Bivalves	Clams, Mytilidae, Cardiidae, Pectinidae, Scaphopoda	0.323	0.302	0.375
Snails	17 species, Buccinidae	0.117	0.072	0.811
Other Crabs	*Hyas* , *Telmessus* , Paguridae, *Paralithodes*	0.437	0.384	0.179
Shrimps	Crangonidae, Hippolytidae, Pandalidae	0.406	0.396	0.197
Sea stars	Solasteridae, Goniopectinidae, Echinasteridae, Asteriidae, Pterasteridae	0.382	0.262	0.357
Brittle stars	*Amphiophiura, Ophiura, Ophiacantha* , and *Ophiopholis*	0.382	0.262	0.357
Basket stars	*Gorgonocephalus*	0.382	0.262	0.357
Urchins, dollars, cucumbers	Clypeasteroida, Holothuroidea, Echinoidea	0.382	0.262	0.357
Sponge	*Halichondria*	0.245	0.112	0.644
Anemones	*Urticina*	0.382	0.262	0.357
Benthic urochordate	*Styela* , *Halocynthia*	0.245	0.112	0.644
Corals	*Gersemia*	0.382	0.262	0.357
Benthic amphipods	Gammaridae, Caprellidae	0.604	0.200	0.196
Polychaetes	All	0.570	0.175	0.255
Worms etc.	Sipuncula, Echiura, Priapula, Nemertea, Brachiopoda, and Bryozoa	0.382	0.262	0.357
Misc. crustaceans	Isopoda, Cumacea, Cirripedia, Pycnogonida, and Ostracoda	0.382	0.262	0.357

Table 3.4: Time series data used for Ecosim manipulation of biomass for phytoplankton, pelagic-benthic coupling (given as proportions of phytoplankton biomass routed to phytoplankton export detritus and phytoplankton retained detritus), terrestrial matter, and bacterial biomass under predicted changes on the Chukchi Sea shelf from 2015 - 2050. 'Pool code' refers to the number of the functional groups in Ecopath, 'Type' to the type of forcing that was set to 'forcing biomass', and numbers 1-4 refer to the simulations.

Simulation	1	2		3	4
Name	Phytoplankton	Phytoplankton export detritus	Phytoplankton retained detrtius	Outside terrestrial detritus	Benthic bacteria
Pool code	55	57	59	56	54
Type	-1	-1	-1	-1	-1
2015	15.0	2600.8	895.1	15.6	26.4
2016	15.0	2571.0	905.3	16.0	27.8
2017	15.1	2541.3	915.5	16.4	29.1
2018	15.1	2511.6	925.8	16.8	30.5
2019	15.2	2481.9	936.0	17.2	31.9
2020	15.2	2452.1	946.2	17.6	33.3
2021	15.3	2422.4	956.5	18.0	34.6
2022	15.3	2392.7	966.7	18.4	36.0
2023	15.3	2363.0	976.9	18.8	37.4
2024	15.4	2333.3	987.1	19.3	38.7
2025	15.4	2303.5	997.4	19.7	40.1
2026	15.5	2273.8	1007.6	20.1	41.5
2027	15.5	2244.1	1017.8	20.5	42.9
2028	15.6	2214.4	1028.1	20.9	44.2
2029	15.6	2184.6	1038.3	21.3	45.6
2030	15.6	2154.9	1048.5	21.7	47.0
2031	15.7	2125.2	1058.8	22.1	48.3
2032	15.7	2095.5	1069.0	22.5	49.7
2033	15.8	2065.7	1079.2	22.9	51.1
2034	15.8	2036.0	1089.4	23.3	52.5
2035	15.9	2006.3	1099.7	23.7	53.8
2036	15.9	1976.6	1109.9	24.1	55.2
2037	15.9	1946.9	1120.1	24.5	56.6
2038	16.0	1917.1	1130.4	24.9	58.0
2039	16.0	1887.4	1140.6	25.3	59.3
2040	16.1	1857.7	1150.8	25.7	60.7
2041	16.1	1828.0	1161.0	26.1	62.1
2042	16.2	1798.2	1171.3	26.6	63.4
2043	16.2	1768.5	1181.5	27.0	64.8
2044	16.2	1738.8	1191.7	27.4	66.2
2045	16.3	1709.1	1202.0	27.8	67.6
2046	16.3	1679.3	1212.2	28.2	68.9
2047	16.4	1649.6	1222.4	28.6	70.3
2048	16.4	1619.9	1232.7	29.0	71.7
2049	16.5	1590.2	1242.9	29.4	73.0
2050	16.5	1560.5	1253.1	29.8	74.4

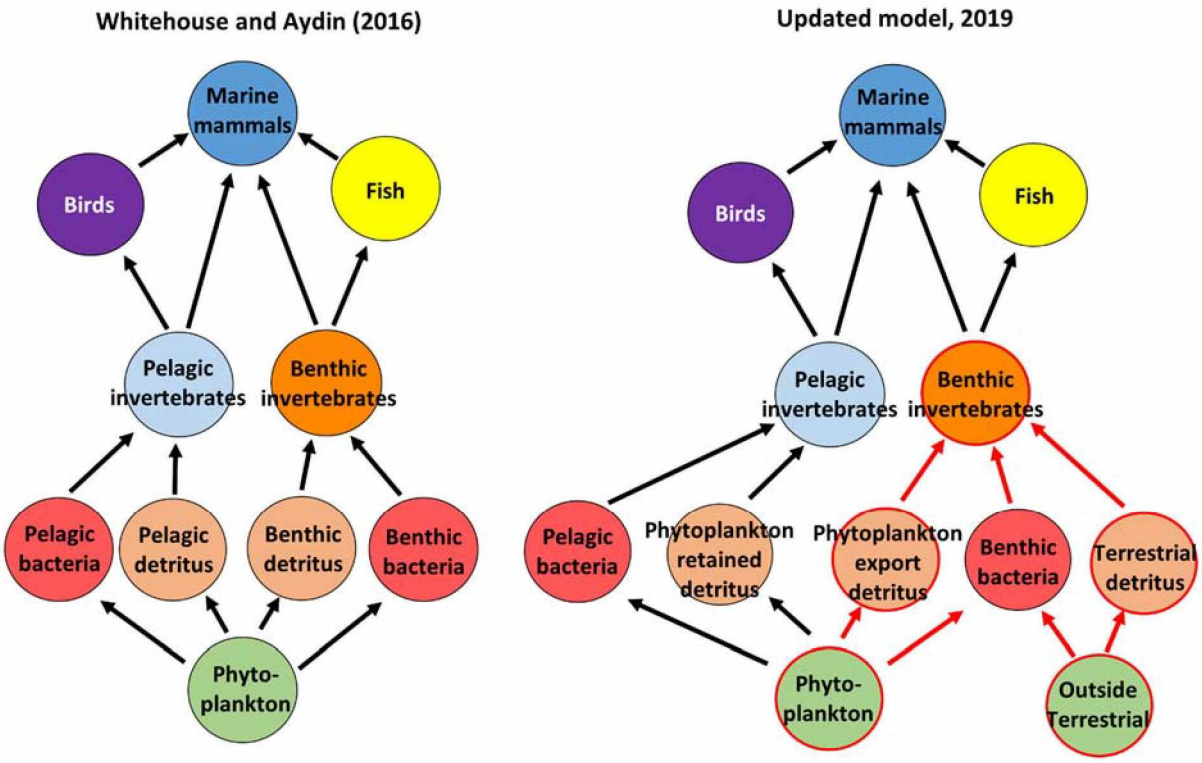


Figure 3.2: Comparative schematic of the original Whitehouse and Aydin (2016) and our updated mass-balanced Chukchi Sea ecosystem model. Arrows indicate feeding connections and flow of energy between larger functional groups. Brown = detrital pools, green = primary producers, red = microbes, orange = benthic invertebrates, light blue = pelagic invertebrates, yellow = fish, purple = birds, and dark blue = marine mammals. Red outline and arrows indicate parameters and functional groups that reflect changes in the updated model.

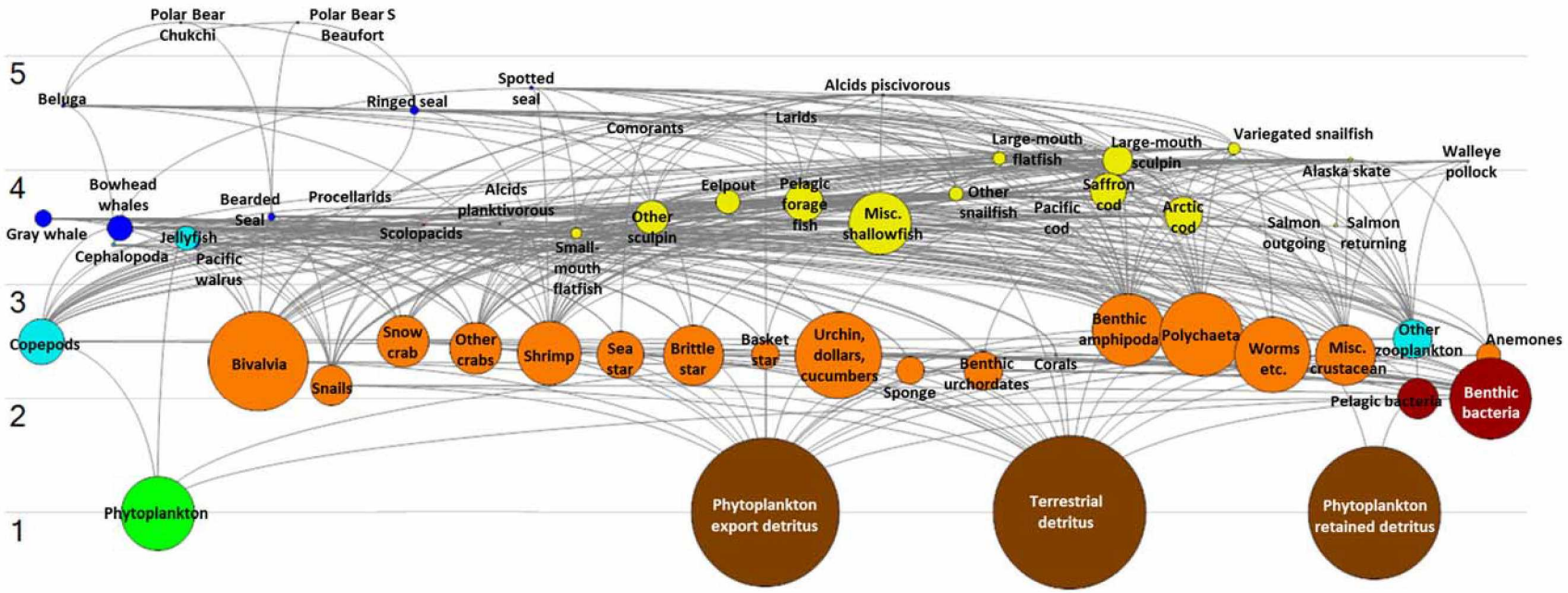


Figure 3.3: Flow chart for the updated mass-balanced Chukchi Sea ecosystem model. Numbers on the left indicate trophic level, size of nodule indicates biomass of respective functional group, gray lines indicate unidirectional feeding connections and energy flow between functional groups, and colors are indicative of larger functional groupings. Brown = detrital pools, green = primary producers, red = microbes, orange = benthic invertebrates, light blue = pelagic invertebrates, yellow = fish, purple = birds, and dark blue = marine mammals.

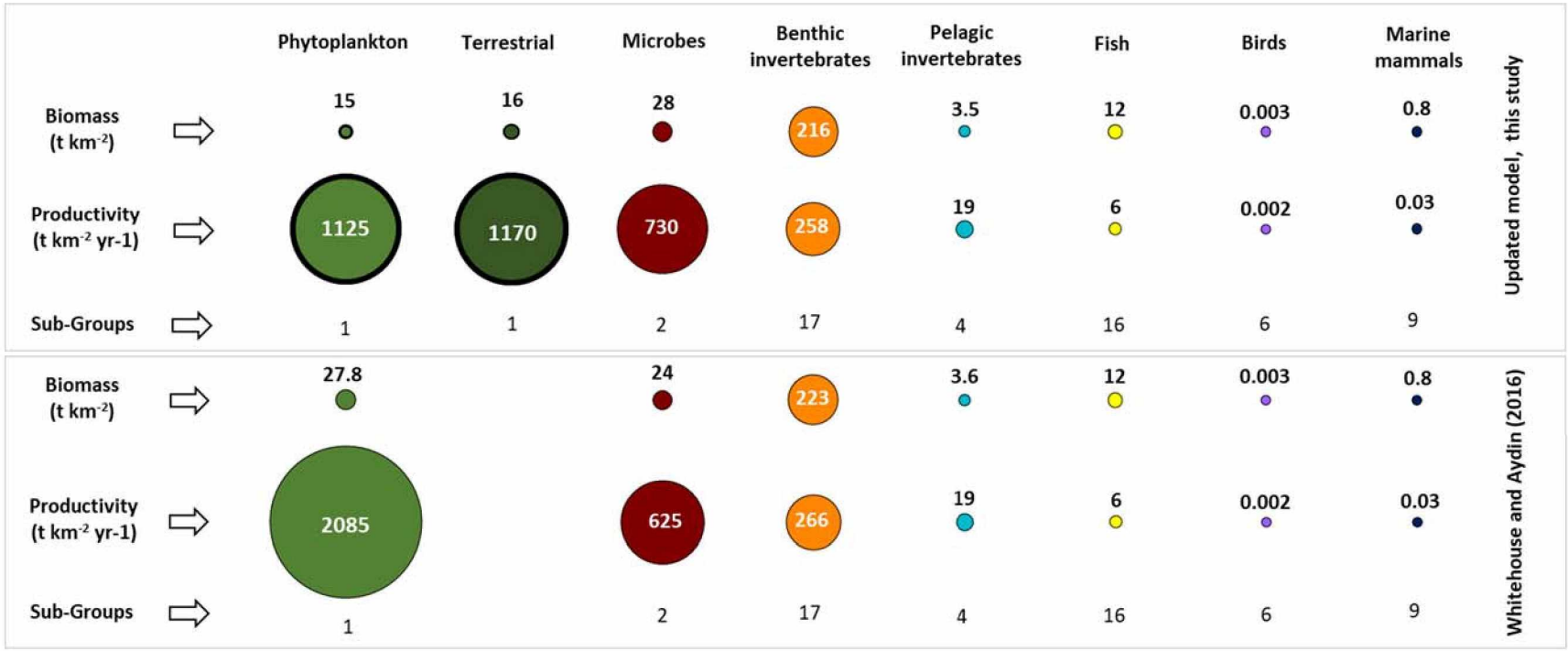


Figure 3.4: Biomass, productivity of larger functional groups in the updated Chukchi Sea ecosystem model (top panel) and the Whitehouse and Aydin 2016 (bottom panel) model. The figure shows cumulative biomass (t km^{-2}), productivity (t km^{-2} yr^{-1}), and number of subgroups included in the group. Size of circles indicates the representative biomass and production value. Thick black outline indicates the groupings that were updated in the current model. Green = primary producers, red = microbes, orange = benthic invertebrates, light blue = pelagic invertebrates, yellow = fish, purple = birds, and dark blue = marine mammals.

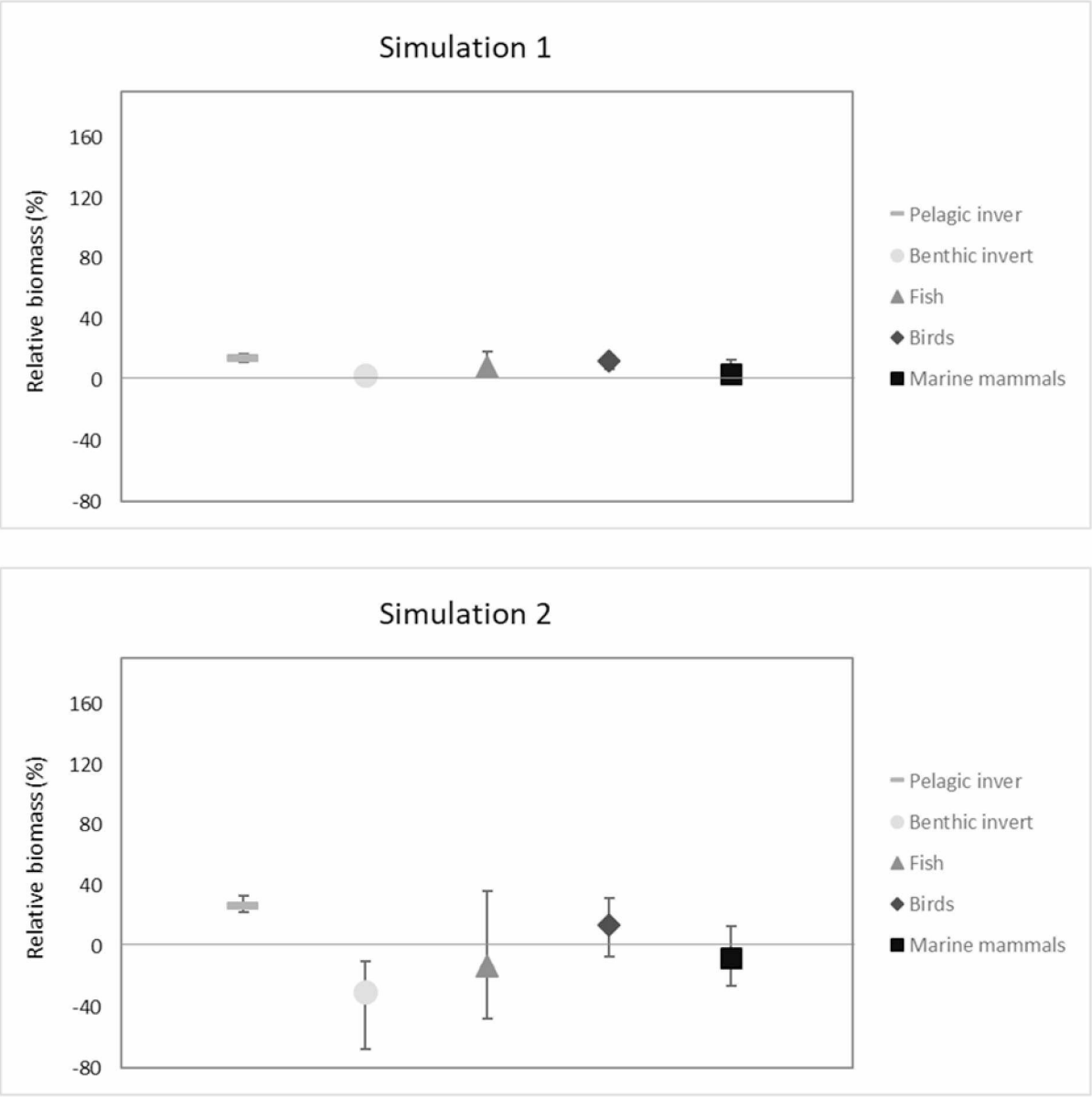
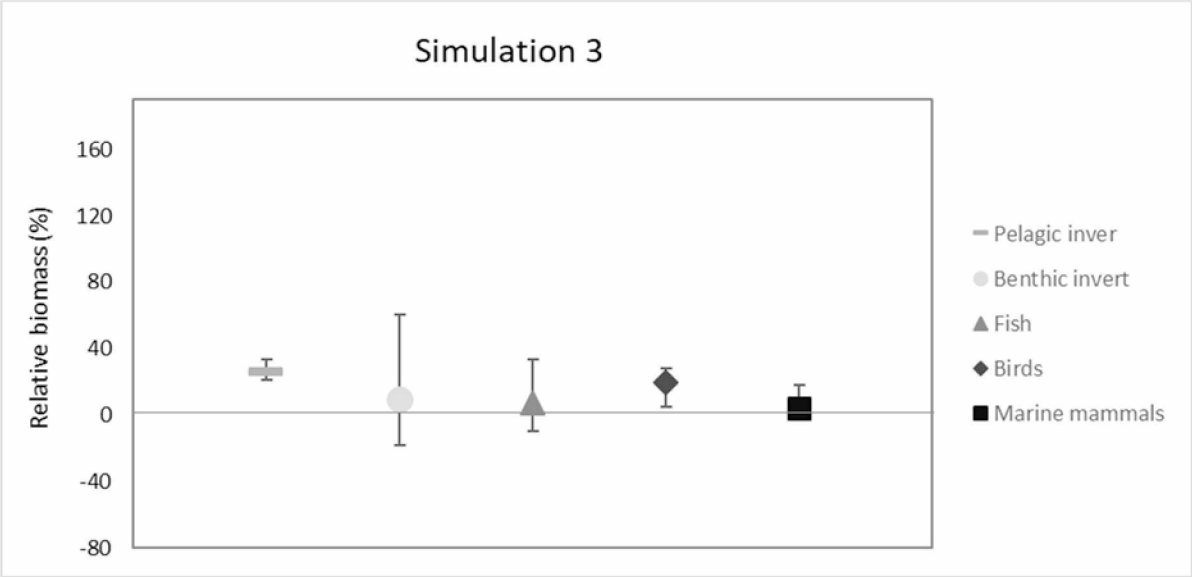
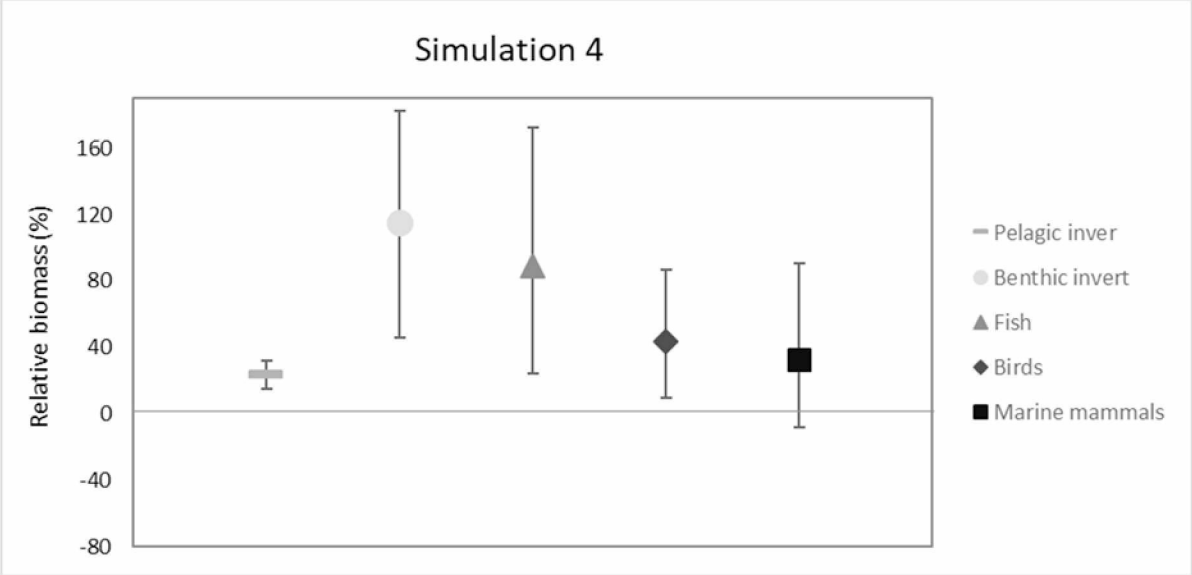


Figure 3.5: Average relative biomass compared to initial biomass (2015) at end of simulation period (2050) based on cumulative Ecosim simulations of the updated mass-balanced ecosystem model of the Chukchi Sea shelf. Error bars for each ecosystem group indicate the minimum and maximum relative biomass values from the functional groups within each ecosystem group (see Fig. 3.3). Simulation 1 refers to an increase in phytoplankton biomass, simulation 2 refers to an additional weakening in pelagic-benthic coupling, simulation 3 refers to an additional increase in terrestrial matter biomass, and simulation 4 refers to an additional increase in microbial production. The gray line indicates steady state situation with no changes in relative biomass from the initial start year (2015).

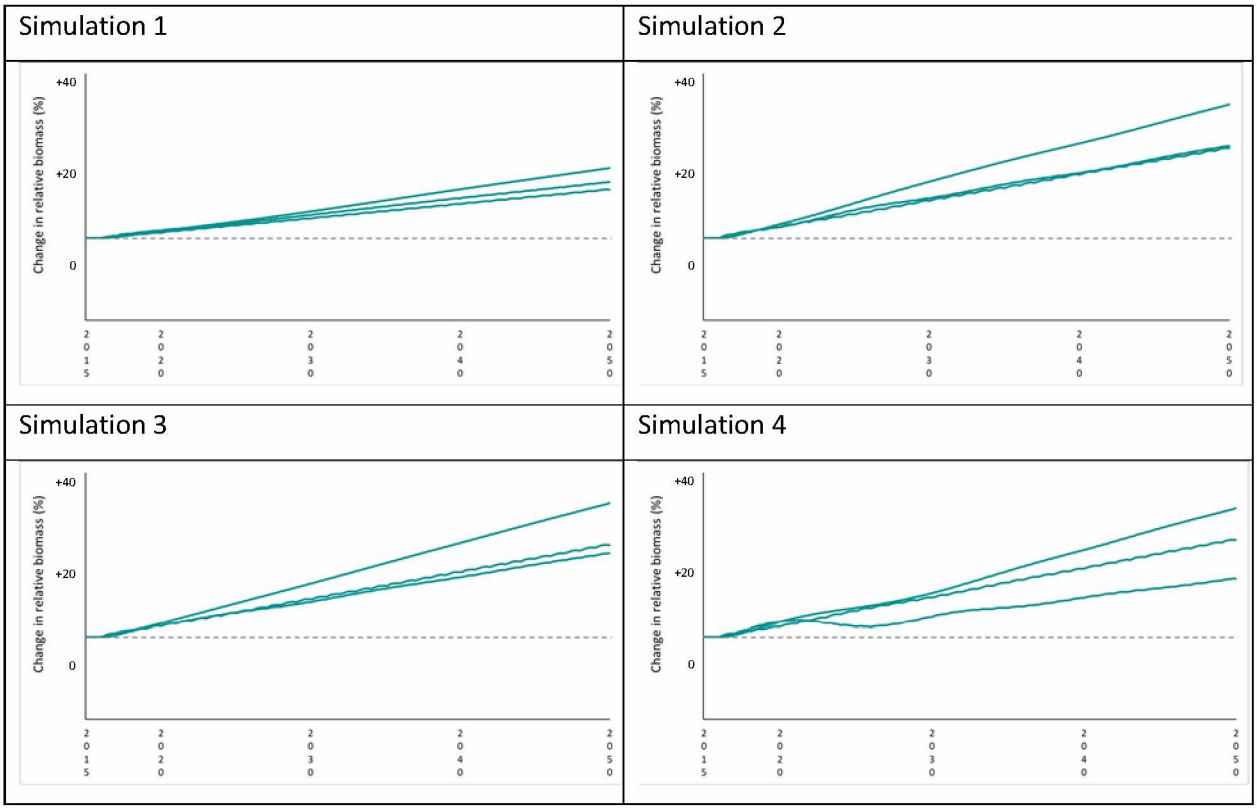
Figure 3.5: continued.





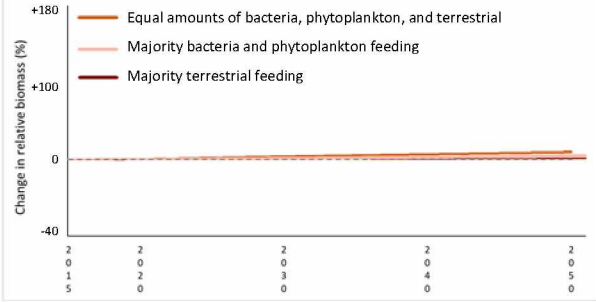
Appendix 3.1: Trends in relative biomass (change from initial biomass) for each major ecosystem group (a-e) across the simulation period (2015-2050) based on Ecosim simulations of the updated mass-balanced ecosystem model of the Chukchi Sea shelf. Simulation 1 refers to an increase in phytoplankton biomass, simulation 2 to a weakening in pelagic-benthic coupling, simulation 3 to an increase in terrestrial matter biomass, and simulation 4 to an increase in microbial production. Each simulation also included the changes of all previous simulations. Different shades within some of the larger taxon group indicate functional groupings based on feeding preferences (see legend). Abbreviations in figures refer to specific ecosystem groups: Benthic invertebrates – S (Snails), BU (Benthic urchordates), Sp (Sponges), SC (Snow crab), Birds – S (Scolopacids), L (Larids), C (Cormorants), Fish – AC (Arctic Cod), S (Salmon), P (Pollock), SMF (Small-mouth flatfish), Sc (Sculpin), Sk (Skates), Mammals – G (Gray whales), W (Pacific walrus), S (Bearded seals).

(a) Pelagic invertebrates

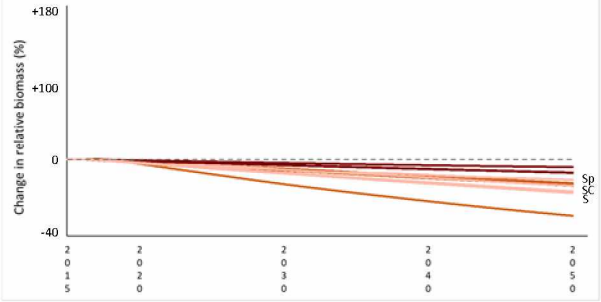


(b) Benthic invertebrates

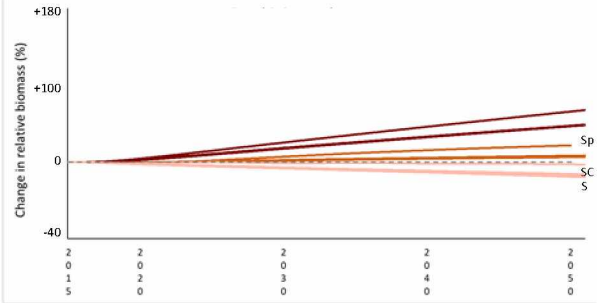
Simulation 1



Simulation 2



Simulation 3



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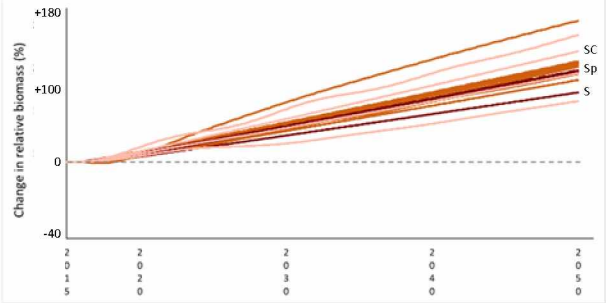
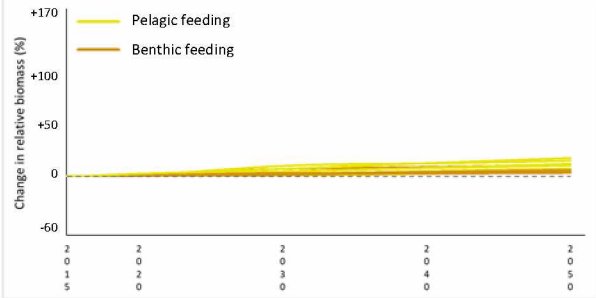


(c) Fish

Simulation 1



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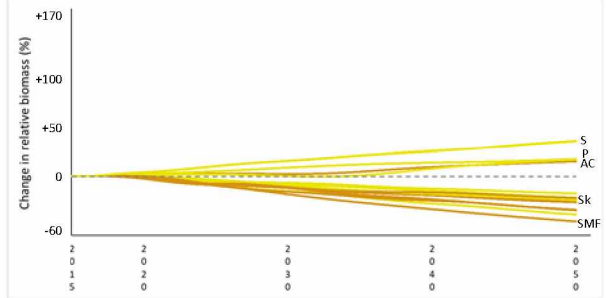
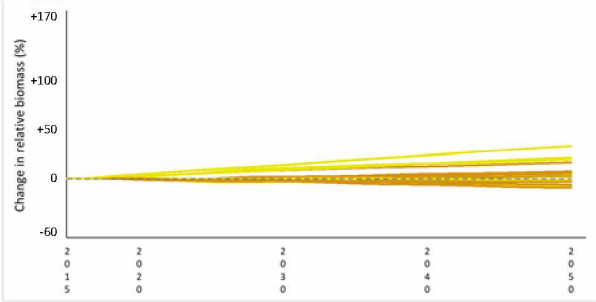


Simulation 3



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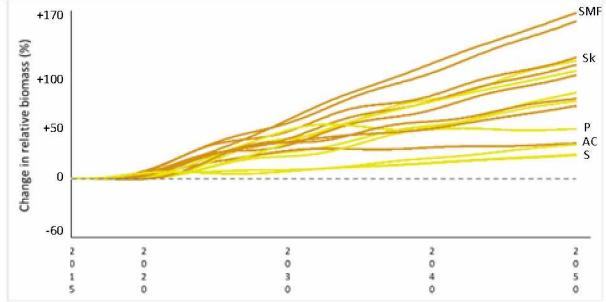
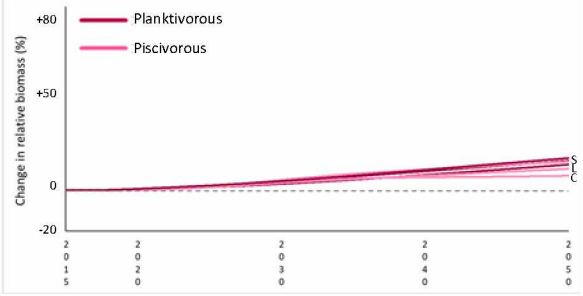


(d) Birds

Simulation 1



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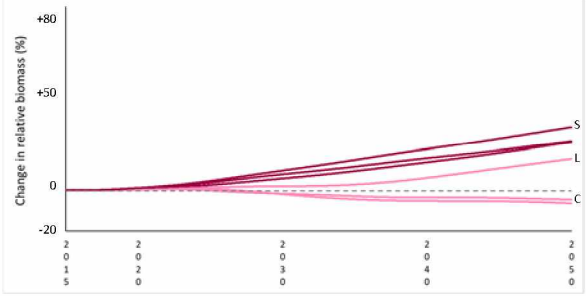

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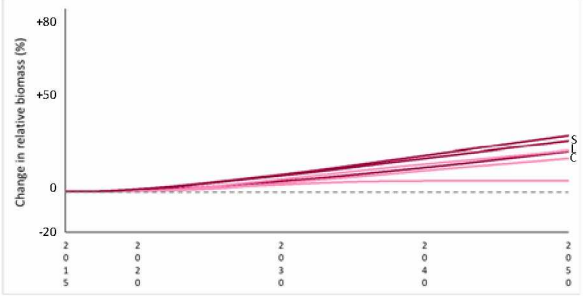
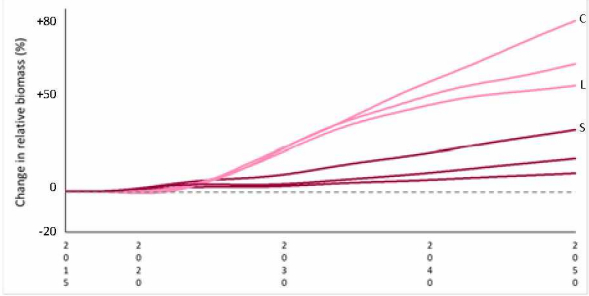
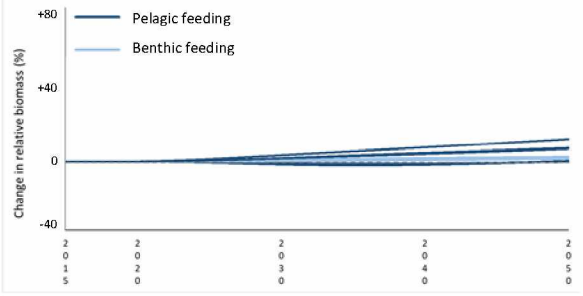


Simulation 4

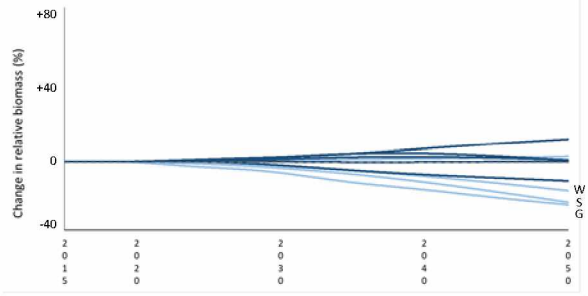


(e) Marine mammals

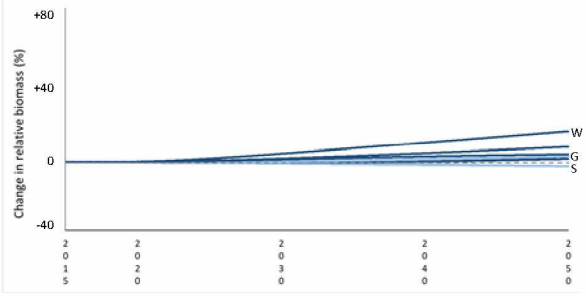
Simulation 1



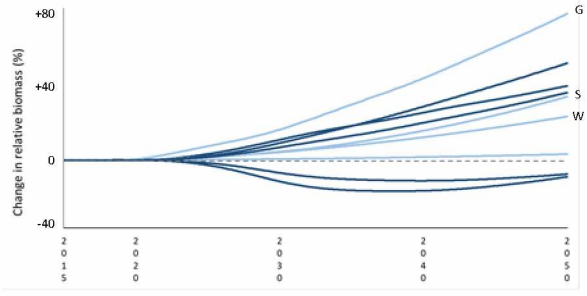
Simulation 2



Simulation 3



Simulation 4



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General conclusion

The results of this study emphasized the importance of organic matter sources other than that derived from phytoplankton production in supporting the Arctic Chukchi Sea shelf ecosystem. Using compound-specific stable carbon isotope values of essential amino acids (EAA), I tracked the relative proportion of bacterial, phytoplankton, and terrestrial EAA into Chukchi Sea shelf sediments and invertebrate diets. High proportions (average ~40 %) of terrestrial EAA in sediments likely originated from surrounding Alaskan rivers and permafrost melt and accumulated in sediments, based on low degradation rates. Increased river discharge and coastal erosion are expected with continued climate warming (Guo et al., 2004; Goñi et al., 2005) and could increase the terrestrial EAA contribution in sediments even further. Concurrently, climate-driven increases in temperature could enhance bacterial production, while possible weakening in pelagic-benthic coupling could decrease the flux of phytoplankton matter to Chukchi Sea sediments. Together, these processes have the potential to change the organic matter composition on the Chukchi shelf, with implications for the benthic feed web depending on the sources.

Overall, EAA sources (bacterial, phytoplankton, terrestrial) of common benthic invertebrate feeding types (FT) were similar across FTs, but some distinct differences were evident among genera within the same FT. This indicated that feeding habits are modulated by different characteristics, in addition to general FT. These characteristics can include mobility, selectivity, and assimilation efficiencies, which should be taken into account when analyzing benthic food webs or larger ecosystem functions. All genera included high proportions of terrestrial EAA in their diets, in part reflecting the abundance of this source in sediments, and supporting other recent findings that terrestrial matter is commonly being used by benthic consumers.

The incorporation of terrestrial organic matter, in addition to phytoplankton production and bacterial biomass as detrital food sources into an existing Chukchi Sea ecosystem model, resulted in diversified energy flow, typically a sign of greater ecosystem stability. Model simulations for a period of 2015-2050 suggested that a weakening in pelagic-benthic coupling results in reduced biomass of benthic-feeding invertebrate and vertebrate taxa, but this reduced energy flow through the benthic food web could be compensated through increased availability of terrestrial matter and bacterial production. However, model simulations did not take into account other climate-related changes in ecosystem functioning, such as changes in metabolic demands of organisms, changes in community composition, or nutritional values of different organic matter sources. These variables should be incorporated into future models.

Climate-driven shifts in the contribution and composition of various organic matter sources to the benthos are likely to have implications on carbon storage and energy flow through the food web. A reduction of phytoplankton-derived matter to benthic food webs is anticipated to negatively impact benthic biomass. This study has shown that other organic matter sources, including terrestrial and bacterial derived organic matter are present in high proportions in Chukchi Sea sediments and are utilized by the rich benthic community. Further, this study showed that enhanced river discharge, coastal erosion, and rising water temperatures could increase the role of terrestrially and bacterially derived matter supporting these food webs. Therefore, this diversification of organic matter sources at the base of the food web has the potential to balance overall system stability in terms of energy flow, as was shown in model simulations.